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# BIOLOGICAL BULLETIN

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## EIGHTY-SEVEN GENERATIONS IN A PARTHENO- GENETIC PURE LINE OF APHIS AVENÆ FAB.

H. E. EWING.

The chief features of my work with *Aphis avenæ* Fab. are here summarized:

1. The pure line theory, as originally applied to self-fertilized plants or asexually reproducing plants and animals, was tested in eighty-seven generations of a parthenogenetic insect.

2. Selections were made for forty-four consecutive generations in an attempt to modify a character that is known to be easily modified by selection in higher animals that reproduce sexually.

3. Variations, both continuous and abrupt, were studied in regard to their transmissibility.

4. The occurrence of pædogenesis is here recorded.

5. The effect of continued parthenogenetic reproduction on the virility and metabolism of a strain has been determined.

6. The effects of temperature on growth, size, reproduction, and dimorphism are here noted.

### INTRODUCTORY CONSIDERATIONS.

About three years ago when the writer began his studies in pure lines, it appeared that the time was quite opportune for some one to carry on breeding experiments with some parthenogenetic insect. Up to that time no one had tested the pure line theory of inheritance in any of the higher arthropods. After attempting breeding work, first with our common cabbage aphid, *Aphis brassicae* Linn., and later with the black cherry aphid, *Myzus cerasi* Fab., I finally started the experiments with *Aphis avenæ* Fab. which are here reported. A very few of the results

obtained with this species have been published,<sup>1</sup> but none of those obtained beyond the first fifteen generations. Here there is given for the first time a complete report of the pure line work with *Aphis avenæ* Fab. up to the last generation obtained, the eighty-seventh. I regret that, at the end of the eighty-seventh generation, excessive heat killed all the individuals of the line; stopping further experimentation which might have given results of even more importance.

Plant lice are especially well adapted for experimental purposes in pure lines. They belong to the order Hemiptera, a group of insects showing a relatively high degree of organization. They can be reared easily on many small succulent plants; are so small that a score or more of their breeding cages can be kept in a small laboratory, yet they are large enough to be easily handled and mounted on microscope slides. Plant lice reproduce very rapidly, and give a sufficiently large number of progeny. The species used gave a new generation every six days with an average number of progeny of from twelve to twenty individuals. *Aphis avenæ* Fab. is in fact so well adapted for pure line work in another respect that it was easily made the choice of the species available in the locality where the experiments were started. This characteristic is its ability to reproduce continually asexually, or parthenogenetically, under the natural conditions found on the Pacific slope—the place where the work was begun. Occasionally sexual forms have been reported from these milder portions of the United States, but never has the present writer found them there. In the north central and in the northeastern states the sexual forms are common as in the case of other species of aphids. The choice of this species has been, I believe, very fortunate, as the results here given will attest.

But to begin with what are our conceptions as to the effect of selection in a pure line? They are simply these: Selection in a pure line of self-fertilized plants or animals, or plants or animals reproducing asexually, no matter for how long carried on does not change the somatic characters that are dependent upon the germplasm. These somatic characters, according to the theory,

<sup>1</sup> "Pure Line Inheritance and Parthenogenesis," *BIOL. BULL.*, Vol. XXVI., pp. 25-35; and, "Notes on Regression in a Pure Line of Plant Lice," *l. c.*, Vol. XXVII., pp. 164-168. (Both published in 1914.)

will unfold themselves generation after generation—within a certain range of variability—in constant conformity with an ancestral type. This type Johanssen terms the genotype. It is simply the type of the race. Theoretically, then, the germ-plasm is as unchangeable as adamant, and selection with all its rigors should in the end leave the race exactly as it was in regard to its inheritable qualities.

In recent years the term pure line has been applied by some workers<sup>1</sup> to the pure strains of cross-fertilized plants or animals, but incorrectly so, I believe. Johanssen did not consider it as so applying; neither did Jennings, or many of the other workers coming after them. Undoubtedly the theory as originally propounded was not construed as applying to cross-fertilized plants or to sexually-reproducing animals. There is no such thing as purity in Johanssen's sense where the melting-pot of amphimixis alloys the germplasm of one individual with the germplasm of another. In 1911 he stated that we had shown, "to excess that phenotypes may seem totally 'pure' and nevertheless be heterogeneous." He further remarks: "Thus constancy as to the phenotype of the progeny is no sure proof for genotypical purity or unity." Indeed how else could it be if we are to assume the frequent presence of multiple unit characters, and thus accept the infinity-factor hypothesis now constantly put forward by Mendélians to explain what appears to be blending in the case of certain hybrid crosses. This distinction becomes doubly important when we consider the confusion and possible causal relation between heterozygosity expressing itself in segregation of characters, even minute, and the appearance of the so-called mutants. It is in relation to mutation, that the pure line advocates have, in the opinion of the present writer, need to be alarmed at the application of the term pure line to a supposedly homozygous pure strain of cross-fertilized organisms.

#### THE EFFECTIVENESS OF SELECTION IN A PARTHENOGENETIC PURE LINE.

In order to test the effectiveness of selection in a parthenogenetic pure line several different sub-lines were bred in isolation.

<sup>1</sup> Pearl for example. See Pearl, 1915, "Seventeen Years Selection of a Character Showing Sex-linked Mendelian Inheritance," *Amer. Nat.*, Vol. XLIX., pp. 595-608.

These sublimes I will refer to as isolated sublimes, or simply isolations. In each of these, selections were carried on for a few or for many generations to see if there was produced any inheritable effect, due to the picking out of individuals showing extreme variation in the character considered.

*Selections Made in an Attempt to Change the Ratio of the Length of the Third Segment of the Antenna to the Fourth Segment.*

*Previous Results. Isolations Nos. 1 and 2.*

The first character used for observing the effects of selection was that of the ratio existing between the lengths of the third and fourth segments of the antenna. For fifteen generations selections were made in an attempt to change the mean of this ratio for the line, which was found to be 1.80 to 1, *i. e.*, it was found that on the average that the third segment was 1.80 times as long as the fourth segment. Selections were made for the first 10 generations in the attempt to increase this ratio. At the end of the tenth generation the fraternal mean was 1.66 to 1, or decidedly less than the mean for the pure line. Selection had here failed utterly to produce any inheritable effects. Various other selections were made, and the results of the selections with this character have been reported in the two short papers previously referred to. In the writer's conclusion, published in the first of these papers, the following statement was made which summarizes the results so far as the effects of selection are concerned in changing the ratio of the length of the third to the fourth segment of the antenna: "Selections from among extreme variants do not alter the mean as obtained for the strain without selection. The fraternal mean of any generation may show a great fluctuation from the mean of the strain, but this fluctuation is not transmitted to following generations."

*Selections Made in an Attempt to Increase the Length of the Cornicles.*

*Isolation No. 3.*

After making selections for fifteen generations using the ratio existing between the length of the third and fourth segments of the antennæ as a character, much time was spent in studying the specimens obtained for characters that were sufficiently variable,

and at the same time suitable in other respects for use in further selection work. It was noticed that the cornicles (honey tubes) were quite variable both in size and shape. Also it was observed that they were fairly well chitinized, and that they did not appreciably shrink while being passed through killing and clearing fluids in preparation for mounting on microscope slides and further that when mounted on microscope slides they could easily be measured. At first I thought that I would take the ratio existing between the length of the cornicles and the length of the body as a suitable character. Then it was noticed that there was some shrinkage of the body due to the action of the killing and clearing fluids, which, at the time, I feared would cause an introduction of serious errors in measurements. For this reason I finally decided to make selections for the purpose of attempting to increase, not relatively, but absolutely, the length of the cornicles. Such selections, it is observed, should not only tend to increase the length of the cornicles in relation to the length of the body, but also to increase the size of the individuals in the line. In other words, two distinct characters are involved in the consideration of variations in the absolute cornicle-length.

Before going into the details of the selections made in this isolation (isolation No. 3) it is probably best that a few words as to methods be given. In all cases the individuals of a fraternity were treated alike, they were placed in the same killing and clearing fluids, and each individual was kept in each fluid about the same length of time. The specimens were all mounted in balsam on microscope slides, and measurements were made with an ocular micrometer. In each instance the individual whose cornicles were to be measured was allowed to produce its progeny before being killed. If it was the one which was to be selected for carrying on the strain its progeny were saved, isolated while yet immature, and reared until they each gave individuals of the next generation. This method of allowing each individual to rear its progeny before being killed (in order to examine the characters) being the one used throughout the experiments here reported. I find that it is one that commends itself for several reasons, among them the following:

(a) Characters can be much better observed, and measured

more accurately in dead, mounted specimens than in live individuals.

(b) The fecundity of the individual is known when the individual is selected, thus obviating the termination of the experiment through the unsuspected sterility or low fecundity of the selected individual.

(c) Permanent mounts of all individuals examined are desirable as a permanent record to be used later in collecting valuable data.

While making selections in isolation No. 3, I decided upon a system of numbering individuals which was used throughout the series of experiments. According to this system each individual is given in reality three numbers which are written together as one. The first of these, which is written much larger than the second, refers to the number of the isolation (*i. e.*, the isolated subline of the main pure line). The second number, which is written much smaller (a subnumber), refers to the generation to which the individual belongs counting from the stem agamic mother that was first isolated from individuals found in nature. The third number, written the same size as the first, refers to the individual's number in the fraternity to which it belongs. Thus  $3_{16} 5$ , written together as a single number for an individual means that this individual belongs to isolation 3 (the isolation here considered), generation 16, and has been given the number 5 as its individual fraternity number to designate it from the other members of the  $3_{16}$  fraternity.

Before starting the selections in this isolation the mean cornicle-length for the line was determined by getting the mean for all the individuals obtained in six previous generations. The mean length of the cornicles of the wingless agamic females was found to be 2.609. The mean length for the winged females was found to be 2.441. Or in other words the cornicles of the wingless agamic females were found to be 1.065 times longer than the cornicles of the winged agamic females. During the process of selection several winged forms were met with. In such instances the measurements of their cornicles were reduced to the denominator of the wingless form simply by multiplying by 1.065.

Selections in isolation 3 were begun in the 15th generation and continued for 11 generations, ending in the 26th. In almost

every instance the individual selected for carrying on the strain had the longest cornicles of any in its fraternity, and in all instances its cornicles were much longer than the mean obtained for the fraternity. The fraternal means obtained run as follows<sup>1</sup>

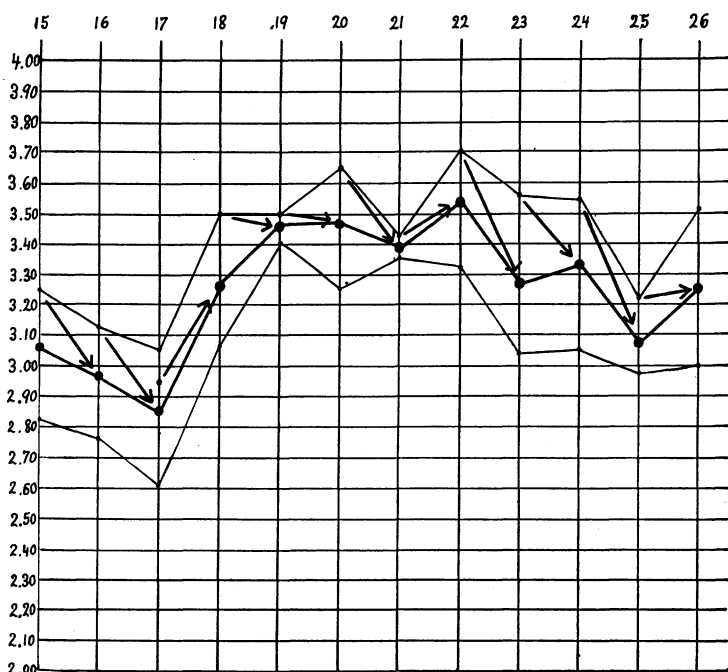


FIG. 1. Graph, or curve, showing the results of selections made in isolation No. 3 in an attempt to increase the length of the cornicles. The heavy middle line joining the large black dots shows the fluctuations of the fraternal means. The light lines show the fluctuations of the extremes of the different fraternities. The arrows show the amount of regression or digression in each case.

beginning with the mean for the 3<sub>15</sub> generation and fraternity: 3.058; 2.979; 2.847; 3.260; 3.463; 3.475; 3.387; 3.510; 3.276; 3.321; 3.083; 3.250. The more complete data obtained for isolation 3 are found in tabular form in Table I.<sup>2</sup>

<sup>1</sup> In the selection work in this isolation an artificial standard of measurement was employed throughout. The number refers to the divisions of the eye micrometer, and they were not reduced to the metric scale. In the subsequent isolations all measurements have been reduced to millimeters, unless specifically stated otherwise.

<sup>2</sup> The computations involved in the preparation of the data in this table and in those which follow were made for the first time by the writer, and were also made later by a student in order to get a check on the results.



TABLE I.

SHOWING MEASUREMENTS OF CORNICLES OF INDIVIDUALS OBTAINED IN ISOLATION 3,  
AND COMPUTATIONS OF THE FRATERNAL MEANS (AVERAGE CORNICLE  
LENGTH FOR EACH FRATERNITY).

Individual.	Average Length of Cornicles.	Winged Forms Corrected.	Fraternal Means.
315I	3.175		
3152	2.675	2.828	
3153	3.250		
3155	2.800	2.980	
			3.058
3162	3.025		
3163	2.600	2.769	
3164	3.000		
3165	3.125		
			2.979
317I	2.450	2.609	
3172	2.875	3.061	
3173	2.550	2.715	
3174	2.950		
3175	2.575	2.740	
3177	2.825	3.008	
			2.847
318I	3.200		
3182	3.075		
3185	3.500		
3186	3.175		
318II	3.350		
			3.260
3192	3.400		
3193	3.275	3.490	
3196	3.500		
			3.391
3202	3.500		
3203	3.550		
3204	3.350		
3205	3.400		
3206	3.250		
3208	3.450		
3209	3.650		
320IO	3.525		
320II	3.550		
320I2	3.525		
			3.475
321I	3.350		
3214	3.425		
			3.387
322I	3.500		
3222	3.525		
3223	3.325		
3225	3.500		
3227	3.700		
			3.510
323I	3.350	3.570	
3232	2.975	3.050	
3233	3.200	3.400	
3235	3.150	3.350	

TABLE I.—*Continued.*

Individual.	Average Length of Cornicles.	Winged Forms Corrected.	Fraternal Means.
3236	3.250		
3237	3.000	3.200	
3238	2.850	3.040	
3239	3.100	3.300	
32310	3.200	3.400	
32311	3.000	3.200	
			3.276
3241	3.450		
3243	3.050		
3244	3.225		
3246	3.475		
3248	3.300		
3249	3.550		
32412	3.200		
			3.321
3253	2.800	2.980	
3256	3.025		
3257	2.925	3.110	
3258	3.025	3.220	
			3.083
3261	3.250		
3262	3.200		
3263	3.475		
3265	3.200		
3266	3.100		
3267	3.525		
3268	3.000		
			3.250

We note that there is a great fluctuation in the fraternal means obtained. During the early selections, disregarding these fluctuations, the general trend appears to be the augmenting of the fraternal means. But during the latter part of the experiment there is a decided drop in the means, and the last one obtained, 3.250, is much below the mean for the whole line. Hence we fail to find in the continuous selection for 11 generations that any permanent effects were produced. But why the great rise and fall in the fraternal means? This I attribute to the great variation in the size of the individuals obtained, which variations were closely correlated with the variations in the absolute cornicle length. The size variation was undoubtedly influenced by the change in temperatures, as I succeeded in demonstrating later. The results of this demonstration will be given beyond in this paper. Selection, therefore, failed to influence in the least the mean length of the cornicles in the pure line of *Aphis avenæ* Fab.

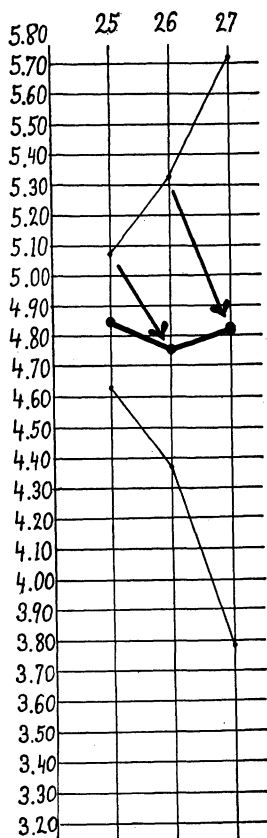


FIG. 2. Plot showing the results of selection in isolation No. 4, for long narrow cornicles. The figures in a column to the left represent the lengths of the cornicles in terms of their widths which in each case is taken as unity. The generations are numbered at the top. Curve plotted as in Fig. 1.

graphically in Fig. 2. The measurements and ratios obtained are given in Table II.

### *Selections Made for Long Narrow Cornicles. Isolation No. 4.*

In this isolation selections were made in an attempt to increase the length of the cornicles in comparison with their width at their distal ends (at the cornicle-ring). Selections for only three generations were made. The first selection was made in the twenty-fifth generation. The ratio expressing the mean for this fraternity was 4.86 (*i. e.*, on the average the cornicles of this fraternity were 4.86 times as long as broad at their distal ends). The individual with the highest ratio,  $4_{25}I$ , was selected from this fraternity. It gave 13 offspring that were reared to maturity. The mean for these 13 offspring (the twenty-sixth generation) was found to be 4.77. This mean is slightly lower than the one for the previous generation. From the twenty-sixth generation, the individual with the highest ratio,  $4_{26}3$ , was selected for obtaining the next generation. It gave the twenty-seventh generation, producing 6 adults with a mean ratio of 4.82, or four hundredths less than that of the mean of the fraternity from which the first selection was made.

We find then that no effects of selection are evident in this isolation. The results obtained for isolation 4 are shown. The measurements and ratios obtained

TABLE II.

SHOWING MEASUREMENTS OF CORNICLES OF INDIVIDUALS OBTAINED IN ISOLATION 4,  
AND COMPUTATIONS OF THE FRATERNAL MEANS (THE AVERAGE RATIO OF THE  
CORNICLE LENGTHS TO WIDTHS FOR ALL MEMBERS OF A FRATERNITY).

Individual.	Average Length of Cornicles.	Average Width of Cornicles.	Ratio of Length to Width.	Fraternal Means.
425 I	47.00	9.25	5.08	4.86
425 2	47.50	9.75	4.87	
425 3	44.00	9.50	4.63	
426 I	47.00	9.50	4.95	
426 2	48.00	10.00	4.80	
426 3	49.25	9.25	5.32	
426 5	48.50	10.00	4.85	
426 6	48.50	10.00	4.85	
426 7	47.00	10.75	4.37	
426 8	50.00	10.50	4.76	
426 9	47.00	9.50	4.95	4.77
426 10	49.25	11.00	4.48	
426 I I	44.50	9.50	4.68	
426 I 2	49.00	11.00	4.45	
426 I 3	47.25	9.50	4.97	
426 I 4	49.25	10.75	4.58	
427 I	45.00	8.00	5.62	
427 2	47.25	10.50	4.50	
427 3	49.50	10.50	4.71	
427 4	45.50	12.00	3.79	
427 6	54.25	9.50	5.71	4.82
427 8	50.50	11.00	4.59	

*Selection Made for Increasing the Body Length,—Isolation No. 5;  
and also Selections Made in a Check Isolation (No. 6) for  
Decreasing the Body Length.*

Because stature, or body length, is one of the most commonly studied of the fluctuating variations, and also because it is a character well known to be inherited in some of our higher animals, I decided to see if by continued selection in a pure line it could be affected. Experiences with isolation No. 3, having taught me that size was influenced easily by temperature changes and probably by other changes also, I decided to eliminate errors from these sources by running a check isolation, or subline. And in order to test more rigorously the effects of selection, in this check strain the shortest individuals were picked out in each instance. Selections were begun in the twenty-sixth generation in each isolated subline, and continued until the thirty-second

generation was obtained. The means obtained for each subline are here written in parallel rows (the measurements being given in millimeters), the two belonging to the same generation being superimposed:

Isolation 5—1.582; 1.909; 1.890; 1.603; 1.135; 1.600.

Isolation 6—1.640; 1.628; 1.763; 1.488; 1.390; 1.180.

Here it is observed that two of the six means obtained in the check isolation 6, in which isolation selections were made from the shortest individuals are actually greater than those for the corresponding generations in isolation 5 where selections were

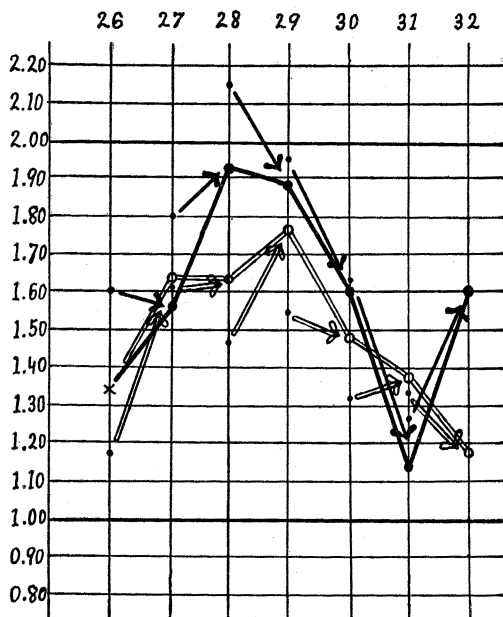


FIG. 3. Plotted curves for check isolations Nos. 5 and 6. In isolation No. 5 (curve represented by heavy line) selections were made for increasing the body length. In isolation No. 6 (curve represented by light open line) which was run as a check to 5, selections were made for decreasing the body length. Graph made on same plan as in previous figures except that fluctuations of extremes are not given.

made from the longest individuals. Further, if we plot the curves of the means obtained for the two sublines together (see Fig. 3), we find that they go up and down together and cross at three different points. The fluctuations in size were found to

TABLE III.

 SHOWING LENGTH MEASUREMENTS OF INDIVIDUALS IN ISOLATION 5 AND CHECK  
 ISOLATION 6, AND THE COMPUTED FRATERNAL MEANS FOR BOTH ISOLATIONS.

Isolation No. 5.			Isolation No. 6.		
Individual.	Length in Millimeters.	Fraternal Mean	Individual.	Length in Millimeters.	Fraternal Mean.
5261	1.15	1.327			1.640
5262	1.48				
5263	1.60				
5265	1.18				
5266	1.24				
5267	1.47				
5268	1.17				
5272	1.80	1.582	6271	1.67	1.628
5273	1.47		6272	1.61	
5274	1.65				
5275	1.62				
5276	1.37				
5281	1.91	1.909	6281	1.81	1.763
5282	1.64		6283	1.65	
5283	2.07		6284	1.85	
5284	1.97		6285	1.32	
5285	1.75		6286	1.67	
5286	1.98		6287	1.47	
5287	1.97				
5288	2.15				
5289	1.88	1.890			1.488
52810	1.77				
5291	1.85	1.890	6291	1.81	1.763
5292	1.94		6292	1.82	
5293	1.95		6293	1.77	
5294	1.84		6294	1.78	
5295	1.87		6295	1.90	
			6296	1.84	
			6297	1.75	
			6298	1.48	
		1.890	6299	1.55	1.488
			62910	1.74	
			62911	1.77	
			62912	1.95	
5301	1.31	1.603	6302	1.72	1.488
5302	1.71		6303	1.32	
5303	1.61		6304	1.64	
5304	1.80		6305	1.34	
5305	1.57		6306	1.54	
5306	1.62		6307	1.52	
			6308	1.38	
			6309	1.44	
		1.603	63010	1.50	1.488

TABLE III.—*Continued.*

Isolation No. 5.			Isolation No. 6.		
Individual.	Length in Millimeters.	Fraternal Mean.	Individual.	Length in Millimeters.	Fraternal Mean
5 <sub>31</sub> 1	1.27		6 <sub>31</sub> 1	1.34	
5 <sub>31</sub> 2	1.00		6 <sub>31</sub> 2	1.45	
		1.135	6 <sub>31</sub> 5	1.38	1.390
5 <sub>32</sub> 2	1.60		6 <sub>32</sub> 1	1.30	
		1.600	6 <sub>32</sub> 2	1.06	1.180

be about as great as before (in isolation 3), but here they *went together*, and were not apparently affected by selection. In the case of isolation No. 5, the final fraternal mean obtained was exactly the same as the length of the first individual selected in this subline. In the case of isolation No. 6, the final mean obtained is found to be just one hundredth of a millimeter more than the length of the first individual selected. The results of the selections in these two check sublines are presented graphically in Fig. 3, and the measurements and some other data obtained are given in Table III.

The results obtained for these six generations show no effects of selection as far as size is concerned. What are the effects of selection on other variable characters?

*Selections Made for Increasing the Length of the Antennæ in Comparison with the Length of the Body. Isolation No. 7.*

It was found that there was a variation not only in the length of the antennæ in comparison with the length of the body, but also a great variation in the absolute length of the antennæ of the different individuals of a fraternity. Since the latter variation involves a complex character, the former was thought to be best adapted for use in selection tests. In isolation No. 7 selections were made in an attempt to increase the length of the antennæ in comparison with the length of the body. They were carried on for five generations. In every case the individual with the longest antennæ in comparison with its body length was selected. The means (which express the ratios existing between the antennal lengths and body lengths) obtained are as

follows, beginning with the twenty-ninth generation:<sup>1</sup> 1:I.257, 1:I.278, 1:I.162, 1:I.178, 1:I.320.

In two instances the fraternal means show the antennal lengths to be greater than they were for the first fraternity obtained. The last fraternal mean obtained, 1:I.320, shows the average

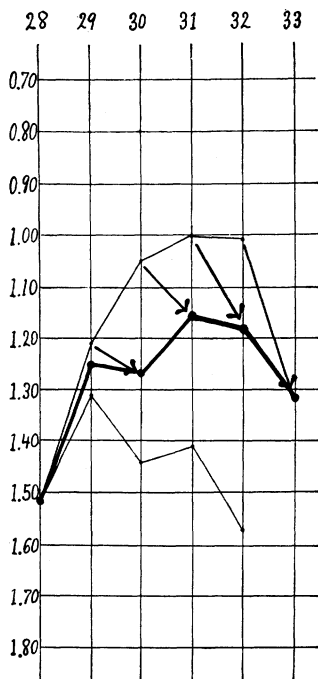


FIG. 4.

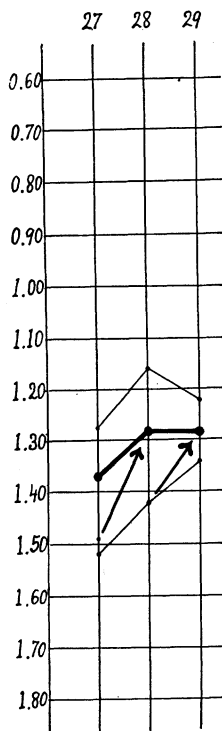


FIG. 5.

FIG. 4. Plotted curve for isolation No. 7. Selections made for increasing the length of the antennæ in comparison with the length of the body. The figures in a column to the left refer to the length of body in terms of the antennal length of the same individual taken as unity. Curve plotted on same plan as in previous figures.

FIG. 5. Results of selections made in isolation No. 8, in the opposite direction from those made in isolation No. 7. Curve plotted on same plan as in Fig. 4.

length of the antennæ in comparison with that of the body to be considerably less than it was in the first fraternity (twenty-ninth generation) obtained, but it was considerably longer than

<sup>1</sup> The length of the antennæ is taken as unity as it is always less than the length of the body.



the antennæ of the parent individual of this fraternity. The stem parent of this isolation, or subline, had a very high antennal ratio, however.

The results of selection in this line are well represented graphically in Fig. 4, which shows the relations of the fraternal means to each other, and to the extreme variants of the different fraternities. Further data in regard to the individuals obtained in isolation 7 are found in Table IV.

TABLE IV.

SHOWING LENGTH MEASUREMENTS OF INDIVIDUALS IN ISOLATION 7, AVERAGE LENGTHS OF THEIR ANTENNÆ, THE RATIO OF BODY LENGTH TO ANTENNAL LENGTH, AND THE COMPUTED RATIO FOR THE FRATERNAL MEAN.

Individual.	Length of Body, Artificial Standard of Measure.	Ave. Antennal Length, Artificial Standard of Measure.	Ratio.	Fraternal Mean.
7291	114	87.0	1.31	1.257
7292	117	90.0	1.30	
7296	121	100.0	1.21	
72917	112	92.0	1.22	
7303	132	106.5	1.24	1.278
7304	131	103.5	1.27	
7306	135	93.5	1.44	
7309	135	97.5	1.38	
73013	132	101.0	1.31	
73014	123	116.0	1.06	
7311	102	101.5	1.00	
7312	115	98.0	1.17	
7313	96	93.0	1.03	1.162
7314	98	96.5	1.02	
7315	119	97.0	1.23	
7316	123	90.5	1.36	
7317	126	89.0	1.42	
7318	117	102.0	1.15	
7319	126	99.5	1.27	
73110	104	96.0	1.08	
73112	109	96.5	1.13	
7321	95	77.5	1.23	1.280
7322	105	82.0	1.28	
7323	100	77.5	1.29	
7324	82	78.5	1.04	
7326	75	71.5	1.05	
7332	95	72.0	1.32	

Again, we fail to see any hereditary influence shown in regard to a fluctuating character, or variation. Further tests were made.

*Selections Made for Shortening the Length of the Antennæ in Comparison with that of the Body. Isolation No. 8.*

In isolation No. 8 selection was made in the reverse direction from that of isolation No. 7, using the same character, *i. e.*, the length of the antennæ in comparison with the length of the body. Only two selections were made, but the fraternal means for both generations showed that the average length of the antennæ was greater than in the fraternity from which the first selection was made, thus showing no inheritance of this fluctuating character. The results for isolation 8 are further explained in Fig. 5 and Table V.

*Selections Made in an Attempt to Increase the Length of the Cornicles in Comparison with that of the Body. Isolation No. 9.*

When selections were made in isolation No. 3 to increase the absolute length of the cornicles, two variable characters were involved. One of these was a partial variation, and the other an individual variation. In isolation No. 9, selections were made in attempting to increase the length of the cornicles in comparison with the length of the body, a simple partial variable. Only three selections were made in this case which gave the following means (which show the ratio of the cornicle-lengths in percentage terms of the body lengths): 21.12 per cent., 16.86 per cent., and 21.09 per cent. The first and the last of these means are considerably above the ratio for the stem progenitor of the subline which was 18.8 per cent. The second fraternal mean was much below the ratio for this stem progenitor.

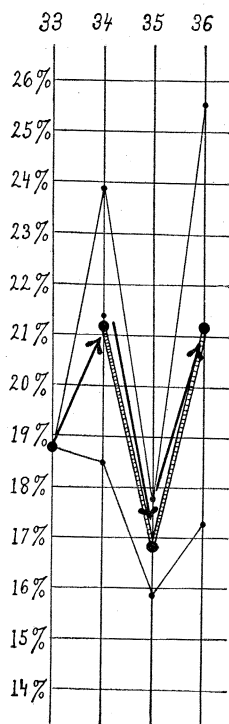


FIG. 6. Plot showing results of selection in isolation No. 9, where an attempt was made to increase the length of the cornicles in comparison with that of the body. The lengths of the cornicles expressed in percentage terms of the body length are found in the column of figures to the left.

TABLE V.

GIVING LENGTH MEASUREMENTS OF INDIVIDUALS IN ISOLATION 8, THE AVERAGE LENGTHS OF THEIR ANTENNÆ, THE RATIO OF BODY LENGTH TO ANTENNAL LENGTH, AND THE RATIO REPRESENTING THE FRATERNAL MEAN.

Individual.	Length of Body Artificial Standard of Measure.	Average Antennal Length, Artificial Standard of Measure.	Ratio.	Fraternal Mean.
8283	121	94.0	1.29	1.290
8284	136	95.5	1.42	
8285	121	103.5	1.17	
8287	123	94.0	1.31	
8292	127	98.0	1.30	1.298
8293	116	87.0	1.33	
8294	126	95.5	1.32	
8295	127	94.5	1.34	
8296	120	97.5	1.23	

The results of the selections in this isolation are in themselves too meager to show anything, but taken together with the results obtained in previous isolated sublines they simply furnish additional proof that selection in a parthenogenetic pure line does not affect hereditarily any of the ordinary individual variations. The meager results obtained for isolation 9 are shown more fully in Fig. 6 and Table VI.

*The Effects of Continuous Selection for Forty-four Generations on a Character that is Known to be Easily Modified by Selection in Animals that Reproduce Sexually.*

All the selections thus far reported were not continued over a very large number of generations, and the results obtained with them may not be convincing to some of our adherents to the belief that selection is effective when made from fluctuating variations and continued for a large number of generations. But if selections are continued for a much longer period do we discover any appreciable effects? In order to give a more thorough test to the effectiveness of selection in a pure line, I decided to make selections for a great many generations using a character that is well known to be inherited in higher animals and plants where cross fertilization takes place. Few characters have been more thoroughly studied or more generally employed in selection

TABLE VI.

GIVING LENGTH MEASUREMENTS OF INDIVIDUALS IN ISOLATION 9, THEIR AVERAGE CORNICLE LENGTH, THE LENGTH OF THE CORNICLES IN PERCENTAGE TERMS OF BODY LENGTH, AND THE COMPUTED PERCENTAGES REPRESENTING THE FRATERNAL MEAN.

Individual.	Length of Body Artificial Standard of Measure.	Average Antennal Length, Artificial Standard of Measure.	Length of Cornicles in Percentage Terms of Body Length.	Fraternal Mean.
9341	112.0	20.75	18.5	21.12
9343	102.5	21.00	20.5	
9345	91.0	21.75	23.9	
9347	102.0	21.50	21.1	
9348	93.0	20.00	21.6	
9349	106.0	22.75	21.5	
9352	104.0	18.50	17.8	
9353	103.0	17.50	17.0	
9355	118.0	18.75	15.9	
9356	124.0	21.50	17.5	16.86
9358	125.0	21.50	17.2	
9361	112.0	22.50	20.1	
9362	119.0	20.50	17.2	
9364	115.0	22.75	19.8	
9366	95.0	20.50	21.6	
9367	108.0	22.00	20.4	
9368	100.0	22.25	22.2	
93611	96.0	23.00	23.9	
93612	90.0	23.00	25.5	21.09
93614	102.0	22.50	22.1	
93616	118.0	21.25	18.0	

work than that of stature, or body length. It was this character that was used by Galton when he formulated his law of regression, and it is a character that is well known to be inherited under the influence of amphimixis. Furthermore, body length is a character the variation of which can be easily measured, and by past experience had proved to be a suitable one to work with for various reasons; hence this one was decided upon.

In isolation 11 selections were made only from among wingless agamic females, in fact after a few generations had been obtained I learned that by controlling somewhat the temperature only such forms appeared. When selections were started in isolation 11 it had been planned to continue them for a hundred generations; and, if by the time the twentieth generation had been obtained no effect of selection had appeared, to change the conditions of the experiment for each subsequent score of generations

except that the selection should continue for increasing the body length, or stature. The reason for doing this was to study the effects of temperature and food upon the character under consideration, especially to see if changing environmental conditions should stimulate any germplasm change. In all 44 generations were obtained. The first score of generations were treated in a definite way, the conditions were considerably changed for the second score of generations, and again changed for the last four generations.

*First Score of Generations; Temperature not Regulated; Growth and Reproduction Period for Each Generation Not Made Uniform.*

For the first score of generations the aphids were reared on young wheat shoots, in large glass vials which were used as breeding cells. They were placed on these young wheat shoots before the same were more than two or three days old. Usually these wheat shoots were less than twenty-four hours old when the lice were placed on them. Each louse was placed on the tender white sheath of the shoot just above the soil. It was sometimes found that after the shoots became a little older and had put out their first leaf that the plant louse would migrate upward and get on this leaf. When such a thing occurred the aphid was always removed to the sheath of the shoot down next to the soil. The breeding cells containing the young wheat shoots and plant lice were kept in the laboratory under such conditions as were found to prevail there. There was a great variation in temperature and a considerable variation in humidity, but Headlee has shown<sup>1</sup> that the latter does not affect the metabolism of aphids when the variations are not greater than would ordinarily occur under laboratory conditions. Further, no definite time was allowed during the first 20 generations for the growth and reproduction period of each fraternity. Individuals were allowed to reach maturity and produce from several to as many as two dozen offspring; then the parent individuals were killed, and measured and selection was made.

Selections in the first score of generations of isolation II were

<sup>1</sup> Headlee, T. J., 1914. "Some Data on the Effect of Temperature and Moisture on the Rate of Insect Metabolism," *Jour. Econom. Ent.*, Vol. VII., pp. 413-417.

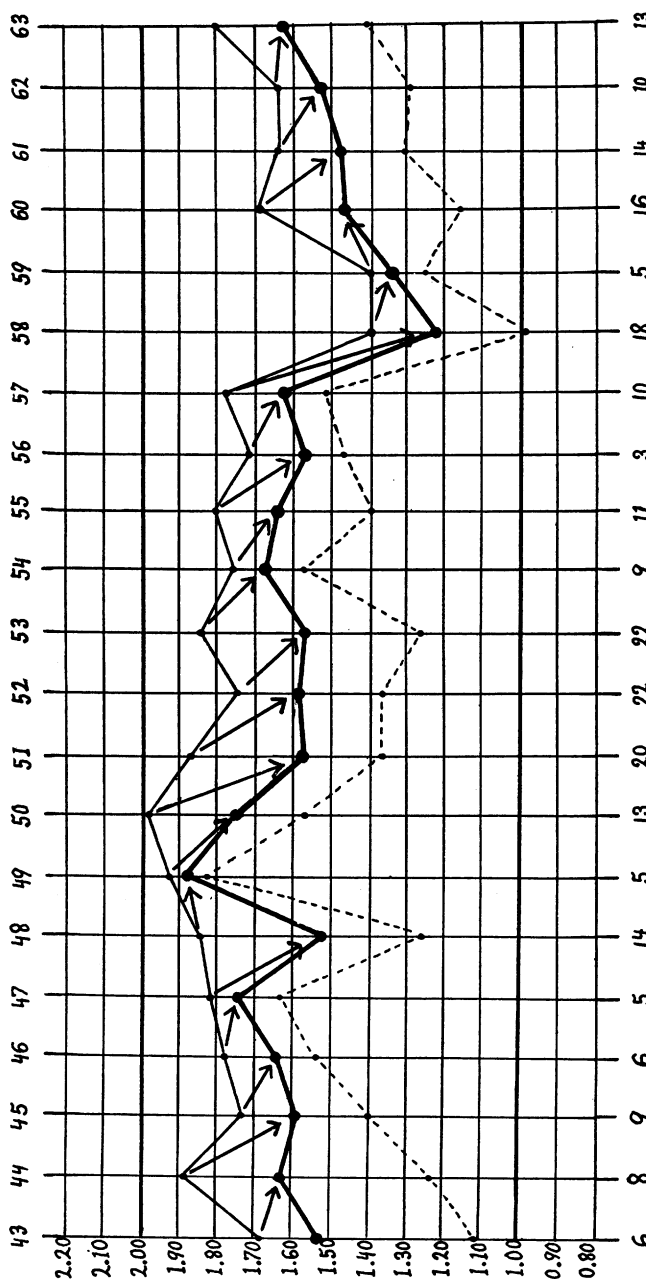


FIG. 7. Plotted results of selections for the first score of generations in isolation No. 11 for increasing the body length. The heavy solid line represents the fluctuations of the fraternal means; the light solid line, the fluctuations of the longest variants; the broken line, the fluctuation of the shortest variants. The amount of regression is indicated by the arrows. Column of figures to left, length of individuals in millimeters. Numbers at top represent the generations; at the bottom, the number of individuals measured in each fraternity.

begun in the forty-third generation, and at the end of the sixty-third generation a total number of 239 adult, wingless individuals had been obtained. In every instance the longest individual was selected from among those of the same fraternity for carrying on the subline. The results of these selections are given graphically in Fig. 7, and in tabular form in Table VII. If we examine the graph, or curve, in Fig. 7, we observe that there is a great fluctuation of the heavy solid line which represents the fluctuations of the means of the succeeding fraternities. The highest mean is 1.882 mm., the mean obtained for the forty-ninth fraternity and the lowest is 1.212 mm., the mean of the fifty-eighth fraternity. The longest individual obtained was 1.99 mm. in length, the shortest obtained was 0.99 mm. in length, or slightly less than one half that of the longest individual.

Looking along the curve, or line which joins the different fraternal means of these 20 generations, and disregarding the fluctuations, we fail to find any general trend upward, and the final mean obtained, 1.617 mm., is but little above the mean with which we started, which was 1.525 mm.; and the next to the last mean obtained, the one for the sixty-second generation, 1.527 mm., is within only two thousandths of a millimeter of the original mean. We conclude, then, that selection had no effect in shifting the mean of the line or strain, which is what Johannsen would call the mean for the *genotype*. But why such great variation in the means of the different fraternities? In the forty-eighth generation and again in the fifty-eighth generation we find a sudden and remarkable drop in the fraternal mean. I observed that in both of these cases the laboratory became quite cold, in fact so cold that it was very uncomfortable to stay in it for any length of time. Hence at the time these means were obtained I supposed that they were so unusually low on account of the low temperature. Later I demonstrated experimentally that a great change in temperature caused a correspondingly great change in the size (hence length) of the individuals.

TABLE VII.

GIVING LENGTH MEASUREMENTS OF INDIVIDUALS OBTAINED IN THE FIRST SCORE OF GENERATIONS OF ISOLATION II, AND THE COMPUTED FRATERNAL MEANS. THE FEW WINGED FORMS THAT APPEARED WERE NOT MEASURED, AND ARE NOT GIVEN IN THIS TABLE.

Individual	Length in Millimeters	Fraternal Mean.
II431	1.56	
II432	1.59	
II433	1.69	
II434	1.56	
II435	1.61	
II439	1.14	
II441	1.81	1.525
II443	1.23	
II444	1.31	
II445	1.73	
II446	1.69	
II447	1.51	
II448	1.80	
II4410	1.89	
II451	1.64	1.621
II452	1.69	
II453	1.69	
II454	1.66	
II455	1.40	
II456	1.43	
II457	1.49	
II458	1.61	
II4510	1.73	
II461	1.57	1.593
II462	1.61	
II463	1.77	
II465	1.61	
II467	1.73	
II469	1.53	
II471	1.63	1.637
II473	1.70	
II474	1.81	
II475	1.76	
II4710	1.80	
II481	1.33	1.740
II482	1.47	
II483	1.56	
II484	1.39	
II485	1.84	
II486	1.33	



TABLE VII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II488	1.81	
II489	1.63	
II4810	1.69	
II4811	1.66	
II4812	1.30	
II4813	1.31	
II4814	1.59	
II4815	1.26	
		1.512
II494	1.87	
II497	1.91	
II498	1.87	
II499	1.83	
II4911	1.93	
		1.882
II501	1.99	
II502	1.61	
II503	1.83	
II504	1.67	
II505	1.69	
II506	1.57	
II507	1.71	
II508	1.83	
II5010	1.63	
II5011	1.77	
II5012	1.64	
II5013	1.97	
II5014	1.74	
		1.742
II511	1.66	
II512	1.41	
II513	1.57	
II514	1.56	
II515	1.66	
II516	1.64	
II517	1.40	
II518	1.64	
II519	1.53	
II5110	1.59	
II5111	1.63	
II5112	1.87	
II5113	1.57	
II5114	1.56	
II5115	1.61	
II5116	1.63	
II5117	1.77	
II5118	1.37	

TABLE VII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II <sub>51</sub> 19	1.41	
II <sub>51</sub> 20	1.53	
		1.580
II <sub>52</sub> 2	1.63	
II <sub>52</sub> 3	1.66	
II <sub>52</sub> 4	1.43	
II <sub>52</sub> 5	1.37	
II <sub>52</sub> 6	1.59	
II <sub>52</sub> 7	1.59	
II <sub>52</sub> 8	1.60	
II <sub>52</sub> 9	1.49	
II <sub>52</sub> 10	1.74	
II <sub>52</sub> 11	1.61	
II <sub>52</sub> 12	1.40	
II <sub>52</sub> 14	1.71	
II <sub>52</sub> 15	1.70	
II <sub>52</sub> 17	1.49	
II <sub>52</sub> 18	1.64	
II <sub>52</sub> 19	1.41	
II <sub>52</sub> 20	1.64	
II <sub>52</sub> 21	1.73	
II <sub>52</sub> 22	1.61	
II <sub>52</sub> 24	1.63	
II <sub>52</sub> 25	1.70	
II <sub>52</sub> 26	1.60	
		1.590
II <sub>53</sub> 1	1.59	
II <sub>53</sub> 2	1.57	
II <sub>53</sub> 3	1.69	
II <sub>53</sub> 4	1.70	
II <sub>53</sub> 5	1.74	
II <sub>53</sub> 7	1.34	
II <sub>53</sub> 8	1.84	
II <sub>53</sub> 9	1.73	
II <sub>53</sub> 10	1.51	
II <sub>53</sub> 11	1.50	
II <sub>53</sub> 12	1.63	
II <sub>53</sub> 13	1.63	
II <sub>53</sub> 14	1.64	
II <sub>53</sub> 15	1.40	
II <sub>53</sub> 16	1.47	
II <sub>53</sub> 17	1.41	
II <sub>53</sub> 18	1.26	
II <sub>53</sub> 19	1.50	
II <sub>53</sub> 20	1.51	
II <sub>53</sub> 21	1.46	
II <sub>53</sub> 24	1.76	
II <sub>53</sub> 25	1.43	
		1.560

TABLE VII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II542	1.74	
II543	1.76	
II544	1.63	
II545	1.66	
II546	1.69	
II547	1.64	
II548	1.61	
II549	1.74	
II5411	1.56	
		1.670
II554	1.67	
II556	1.60	
II557	1.67	
II559	1.40	
II5511	1.61	
II5513	1.56	
II5518	1.57	
II5519	1.66	
II5521	1.77	
II5524	1.73	
II5525	1.80	
		1.640
II568	1.71	
II5614	1.47	
II5616	1.53	
		1.570
II571	1.63	
II572	1.60	
II573	1.51	
II575	1.59	
II579	1.73	
II5711	1.77	
II5712	1.59	
II5713	1.53	
II5715	1.71	
II5716	1.66	
		1.632
II581	1.36	
II582	1.30	
II583	1.14	
II584	1.33	
II585	1.29	
II587	1.10	
II588	0.99	
II589	1.06	
II5810	1.24	
II5811	1.40	
II5812	1.36	
II5813	1.17	

TABLE VII. (continued).

Individual	Length in Millimeters	Fraternal Mean,
II68I4	I.30	
II68I5	I.19	
II68I6	I.11	
II68I7	I.10	
II6820	I.04	
II6821	I.34	
		I.212
II69I	I.27	
II692	I.24	
II693	I.40	
II694	I.37	
II695	I.39	
		I.334
II60I	I.50	
II602	I.41	
II603	I.16	
II604	I.41	
II605	I.41	
II606	I.54	
II607	I.46	
II608	I.53	
II609	I.44	
II6010	I.43	
II6011	I.56	
II6013	I.59	
II6014	I.57	
II6015	I.69	
II6017	I.44	
II6018	I.21	
		I.459
II61I	I.51	
II612	I.47	
II613	I.50	
II614	I.46	
II615	I.47	
II616	I.63	
II617	I.30	
II619	I.51	
II6110	I.54	
II6111	I.33	
II6112	I.46	
II6113	I.41	
II6114	I.53	
II6115	I.47	
		I.471
II62I	I.50	
II622	I.54	
II623	I.64	
II624	I.54	

TABLE VII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II 825	1.51	
II 826	1.54	
II 827	1.57	
II 828	1.63	
II 829	1.29	
II 8210	1.51	
		1.527
II 831	1.76	
II 832	1.80	
II 833	1.54	
II 834	1.74	
II 835	1.49	
II 836	1.71	
II 837	1.56	
II 838	1.70	
II 839	1.57	
II 8310	1.43	
II 8311	1.41	
II 8312	1.71	
II 8313	1.61	
		1.617

*Second Score of Generations; Temperature so Regulated that only Wingless forms Produced, a Six-day Interval Being Allowed for Growth and Reproduction of Each Generation.*

For the second score of generations it was decided to make the conditions of the experiment more definite. Having learned the effect of temperature on the size of the individuals, it was decided to place them in a room where the temperature was less variable. This was done and temperature records were taken daily. During the whole of this part of the experiment no such variations in temperature were allowed as those which affected the first score of generations. By means of experiments elsewhere reported, I learned that under suboptimum growth conditions the winged forms would not appear. The optimum temperature for the wingless forms was found to be about 65° F. So well was the temperature controlled for the second twenty generations that not a single winged form appeared during the entire subexperiment. It was further decided that the same period of time should be allowed for growth and reproduction in each generation. The period allowed was 6 days.

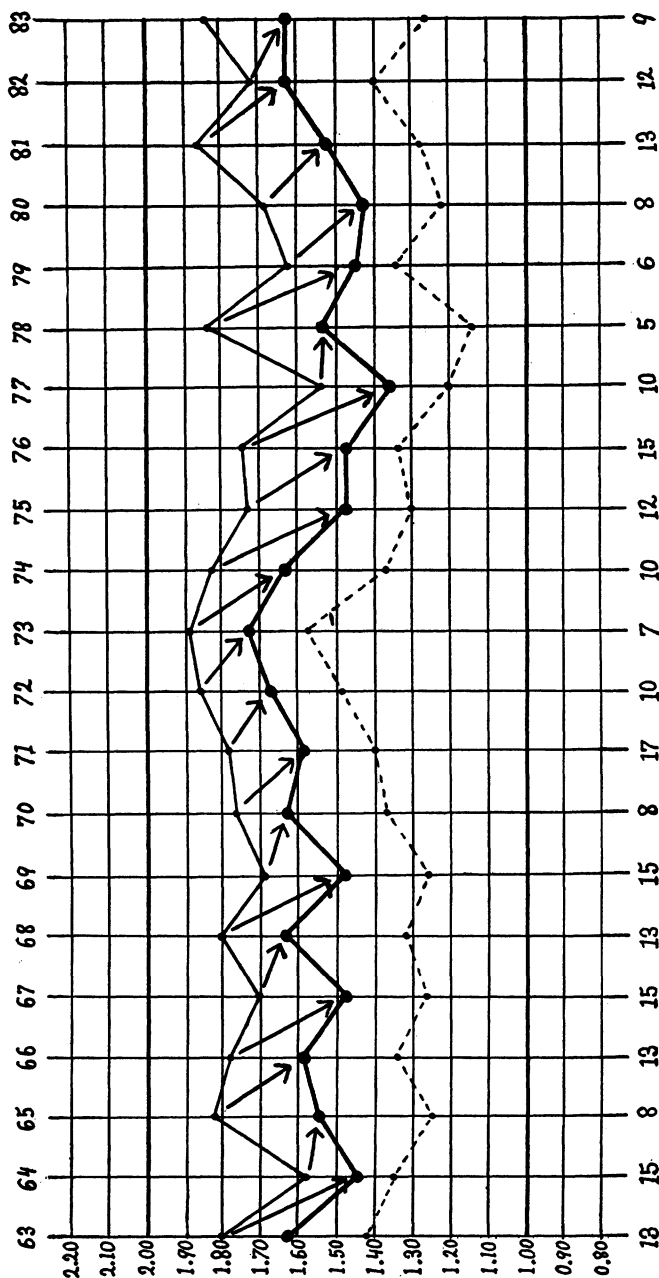


FIG. 8. Plotted results of selection in the second score of generations of isolation No. 11. Curves plotted on the same plan as in Fig. 7.

The results obtained under these more definite conditions are shown in Fig. 8 and Table VIII. By comparing these results with those obtained for the first 20 generations we note, first of all, much less fluctuation in fraternal means. We note that the extreme variants do not vary nearly as much from the mean of the line as they did in the first 20 generations.

We find that the heavy line in Fig. 8 joining the various fraternal means shows no general trend upwards, so we conclude that selection has produced no perceptible inherited change in body length. The last mean obtained, 1.611 mm., is just 6 thousandths of a millimeter less than the mean of the fraternity started with, 1.617 mm.

*The Effect of the Use of Older Wheat Plants, the Last Four Generations of Isolation No. 11.*

During the last 4 generations of subline 11 the aphids were reared on wheat plants several days older than those previously used. During the first and second score of generations the young aphids were placed on wheat shoots to be reared when these shoots were barely out of the soil. In almost every case the first leaf had not been put out. Most of these shoots were less than twenty-four hours old when the aphids were placed on them. In the last four generations all of the wheat plants were several days older. They were from 5 to 11 days old when the young aphids were added, and by the time these insects reached maturity and gave birth to their progeny most of these plants were two weeks old or older.

The offspring of 11<sub>83</sub>1 were the first to be placed on these older wheat plants. After reaching maturity their lengths were obtained and the fraternal mean computed. It was found to be 1.343 mm., a big drop from that of the previous fraternity, which was 1.611 mm. The means of the three following generations were also greatly below this point and the mean of the line. The last mean obtained for these 4 generations and for the whole subline, or isolation 11 was 1.107 mm., which it is observed is greatly lower than any mean previously obtained and only 11 hundredths of a millimeter above the lowest variant obtained in all the first 40 generations where younger wheat shoots were used.

TABLE VIII.

CONTINUATION OF DATA FOR ISOLATION II.—SECOND SCORE OF GENERATIONS.

Individual	Length in Millimeters	Fraternal Mean.
II642	1.50	
II643	1.51	
II644	1.36	
II645	1.50	
II646	1.47	
II647	1.41	
II648	1.41	
II649	1.39	
II6410	1.47	
II6411	1.40	
II6412	1.44	
II6413	1.39	
II6414	1.44	
II6415	1.59	
II6416	1.43	
II651	1.81	1.447
II652	1.64	
II653	1.64	
II654	1.26	
II655	1.49	
II656	1.37	
II657	1.51	
II658	1.67	
II661	1.39	1.549
II663	1.70	
II664	1.47	
II665	1.77	
II666	1.77	
II667	1.43	
II668	1.69	
II669	1.66	
II6610	1.49	
II6611	1.46	
II6612	1.79	
II6613	1.74	
II6614	1.34	
II671	1.61	1.592
II672	1.27	
II673	1.49	
II674	1.60	
II675	1.27	
II676	1.50	
II677	1.70	
II678	1.56	



TABLE VIII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II679	1.51	
II6710	1.29	
II6711	1.60	
II6712	1.64	
II6713	1.38	
II6714	1.46	
II6715	1.44	
		1.487
II681	1.77	
II682	1.73	
II683	1.40	
II684	1.80	
II685	1.64	
II686	1.70	
II687	1.50	
II688	1.31	
II689	1.76	
II6810	1.36	
II6811	1.77	
II6812	1.60	
II6813	1.66	
		1.615
II691	1.44	
II692	1.69	
II693	1.36	
II694	1.50	
II695	1.60	
II696	1.53	
II697	1.41	
II698	1.53	
II699	1.67	
II6910	1.40	
II6911	1.61	
II6912	1.47	
II6913	1.54	
II6914	1.31	
II6916	1.26	
		1.488
II701	1.64	
II702	1.37	
II704	1.63	
II705	1.76	
II706	1.63	
II708	1.60	
II7010	1.64	
II7011	1.67	
		1.617
II711	1.44	
II712	1.50	

TABLE VIII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II713	1.57	
II714	1.79	
II715	1.59	
II716	1.53	
II717	1.66	
II718	1.60	
II719	1.66	
II7110	1.54	
II7112	1.66	
II7113	1.40	
II7114	1.64	
II7115	1.60	
II7116	1.69	
II7117	1.70	
II7118	1.49	
		1.592
II721	1.71	
II722	1.71	
II723	1.51	
II724	1.66	
II725	1.66	
II726	1.67	
II727	1.69	
II728	1.49	
II729	1.86	
II7210	1.77	
		1.673
II731	1.57	
II732	1.81	
II733	1.61	
II734	1.89	
II735	1.64	
II736	1.67	
II737	1.84	
		1.718
II741	1.81	
II744	1.64	
II745	1.40	
II746	1.49	
II747	1.63	
II748	1.79	
II749	1.63	
II7410	1.37	
II7411	1.59	
II7412	1.79	
		1.614
II751	1.50	
II752	1.44	

TABLE VIII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II763	1.54	
II764	1.41	
II765	1.39	
II766	1.34	
II767	1.54	
II768	1.46	
II7610	1.34	
II7611	1.69	
II7612	1.73	
II7613	1.30	
II761	1.44	1.473
II762	1.44	
II764	1.46	
II765	1.33	
II766	1.74	
II768	1.56	
II769	1.36	
II7610	1.47	
II7611	1.46	
II7612	1.60	
II7613	1.41	
II7614	1.33	
II7615	1.46	
II7616	1.54	
II7618	1.43	1.469
II771	1.53	
II772	1.36	
II773	1.44	
II774	1.39	
II775	1.20	
II776	1.24	
II777	1.39	
II779	1.34	
II7710	1.34	
II7711	1.49	
II781	1.84	1.372
II783	1.14	
II784	1.34	
II786	1.73	
II788	1.54	
II791	1.34	1.518
II792	1.51	
II793	1.61	
II794	1.43	

TABDE VIII. (continued).

Individual	Length in Millimeters	Fraternal Mean.
II 795	1.53	
II 796	1.36	
		1.463
II 801	1.69	
II 802	1.34	
II 803	1.33	
II 804	1.50	
II 805	1.46	
II 806	1.36	
II 807	1.37	
II 808	1.21	
		1.407
II 811	1.36	
II 812	1.57	
II 813	1.37	
II 814	1.63	
II 815	1.43	
II 816	1.86	
II 817	1.59	
II 818	1.50	
II 819	1.46	
II 8110	1.34	
II 8111	1.50	
II 8112	1.77	
II 8113	1.27	
		1.511
II 821	1.71	
II 822	1.69	
II 823	1.40	
II 824	1.59	
II 825	1.69	
II 826	1.59	
II 827	1.69	
II 828	1.63	
II 829	1.69	
II 8211	1.43	
II 8212	1.63	
II 8213	1.60	
		1.612
II 831	1.84	
II 832	1.59	
II 833	1.54	
II 834	1.69	
II 835	1.69	
II 836	1.26	
II 837	1.79	
II 838	1.49	
II 839	1.61	
		1.611

The results obtained for these last 4 generations of subline 11 are further illustrated in Fig. 9 and Table IX. Older plants, therefore, cause a remarkable diminution in the size of *Aphis avenæ* individuals. Perhaps it is because these aphids are not able to extract as much food from the harder tissues of older plants, but it may be due to a change in the nature of the juices sucked from the food plant, or due to both of these causes.



FIG. 9. Plotted results of selection in the last four generations of isolation No. 11. Curves plotted on the same plan as in Figs. 7 and 8.

#### The Effects of Selection for 44 Generations on a Fluctuating Variation.

The results of selection in the whole subline 11 are shown graphically in Fig. 10. Here we have plotted the exact lengths of each individual selected, scale  $\times 50$ , and also the lengths representing each fraternal mean, plotted to the same scale. The barred vertical columns represent the lengths of the individuals selected, and the solid vertical columns represent the lengths expressed by the fraternal means. These two kinds of columns are arranged in the diagram Fig. 10 so that the two belonging to the same generation come in pairs, the number of the generation being given at the top of the dotted vertical guide line. The

curved arrows, each of which passes from the top of the column representing the length of the individual selected, to the top of the column representing the length of the mean of its offspring in the next generation, shows the amount of regression, or digression, as the case may be, for the fraternal mean in question.

If we examine this figure we find that with but a single exception there is a dropping of the fraternal mean downward. The

mean of the fraternity for the sixtieth generation is found to represent a length slightly greater than that of the parent of this fraternity.

Is there any evidence of inheritable effects of selection in this long pedigree of 44 generations? Our only conclusion must be in the negative. There is not the least evidence of a general trend upward in the fraternal means as we advance generation

TABLE IX.

CONTINUATION OF DATA FOR ISOLATION II.—LAST FOUR GENERATIONS.

Individual	Length in Millimeters	Fraternal Mean,
II 84I	1.47	
II 845	1.17	
II 846	1.51	
II 849	1.24	
II 8410	1.27	
II 8411	1.40	
		1.343
II 852	1.54	
II 853	1.36	
II 854	1.47	
II 855	1.10	
II 856	1.36	
II 857	1.01	
		1.307
II 861b	1.54	
II 862b	1.39	
II 863b	1.40	
		1.443
II 875	0.99	
II 876	0.97	
II 877	1.36	
		1.107

after generation in this isolated subline. The fluctuations are many and at times great, but the series continues on in the same general way. These fluctuations have been partially analyzed, and in those cases where extremely low or high variations occurred they were found to depend upon environmental conditions (temperature and food supply chiefly). If there is a cumulative effect in selecting extreme variants of each fraternity for a large series of generations, the results obtained in this long series of my pure line of *Aphis avenæ* Fab. fail to show it.

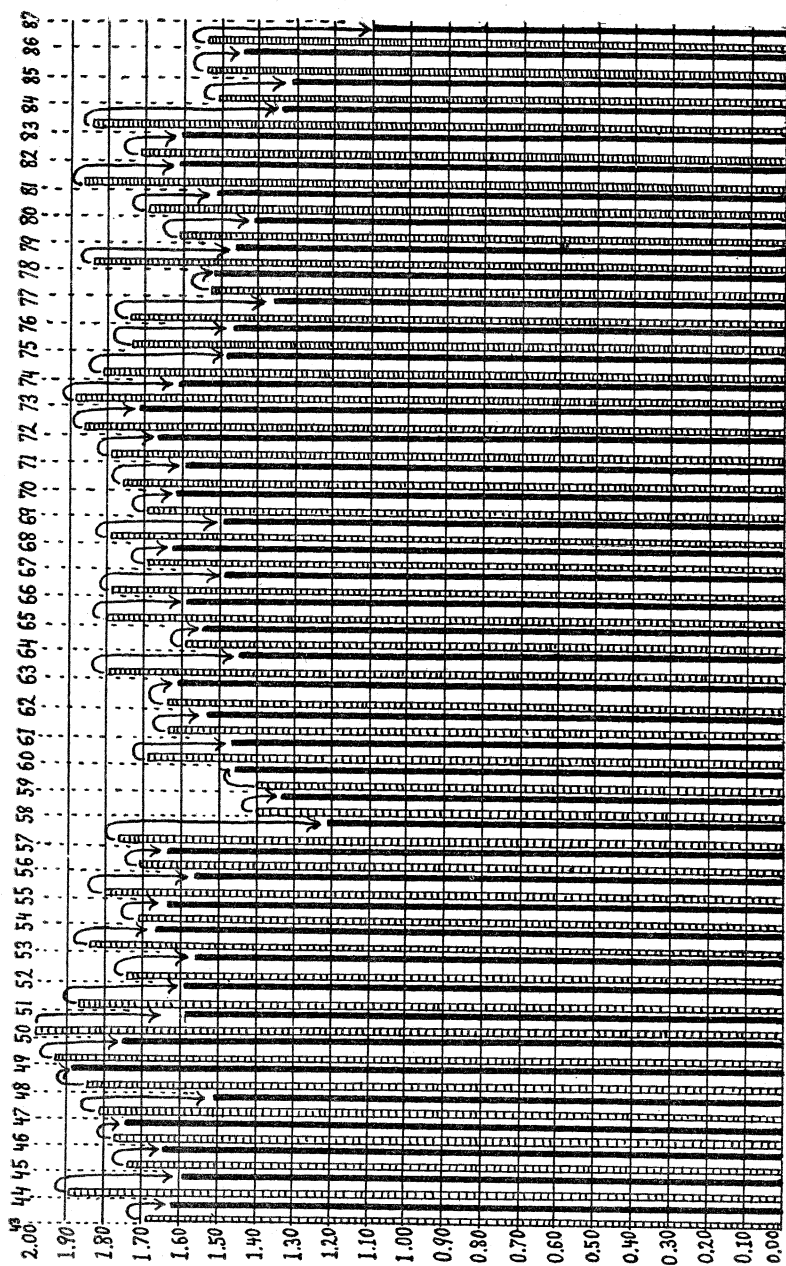


FIG. 10. For explanation see text, page 88.

# THE EFFECTS OF CONTINUED PARTHENOGENETIC REPRODUCTION ON THE VIRILITY AND METABOLISM OF A STRAIN.

Whether or not long-continued asexual reproduction will affect the virility of a strain of animals has long been a debated question. The time was when zoölogists in general held that conjugation or some form of amphimixis was absolutely necessary in order to prevent the eventual dying out of a strain of animals that had long been reproducing asexually. The more recent work of Woodruff,<sup>1</sup> however, has shown us that in the case of *Paramæcium*, at least, conjugation is not necessary in order to rejuvenate a race. The question that next suggests itself is; can insects reproduce indefinitely by means of parthenogenesis? Probably the prevailing opinion among entomologists has been that parthenogenesis could not continue indefinitely in any species of the insects. Certain it is that in all those well-studied species where parthenogenesis is known to occur males have been found to exist. In fact, we find that frequently the parthenogenetic offspring are all males, and are produced thus according to definite law. Further, in the case of some insects, as aphids, males are produced according to the season. On the other hand, in the case of some insects that have not been sufficiently studied, males are unknown. In some of the species of *Thysanoptera* females have been found by hundreds, yet no males are known. In the case of our common pear-slug saw-fly, *Eriocampoides limacina* Retzius, I have counted hundreds, and reared scores of individuals without ever seeing a male, yet males are supposed to exist. Males must be extremely rare in the case of our common oyster-shell scale, *Lepidosaphes ulmi* Linn. I have reared scores and examined thousands of individuals without ever finding a male; however, the male has been described.

Since taking up this work with *Aphis avenæ* Fab., I have observed this species to pass the entire winter on the *Pacific coast* in the agamic form, and, as a matter of fact, have never observed the sexual form in that region of the country, although it probably exists there to a limited extent. We have several experiments on record of aphids having been reared partheno-

<sup>1</sup> Woodruff, L. L. For a review of the work of Woodruff see, Middleton, A. R., 1913, "Work on Genetic Problems in Protozoa at Yale," *Amer. Nat.*, Vol. XLVII., pp. 434-439.



genetically for more than half a hundred generations, but in such cases, I believe, no checks have been made to see if deterioration of the stock was taking place.

After breeding *Aphis avenae* Fab. for 73 generations parthenogenetically, I found the species breeding at Ames, Ia., on oats and barley that was being raised for experimental purposes. I decided to start a check strain with these Iowa forms to see if

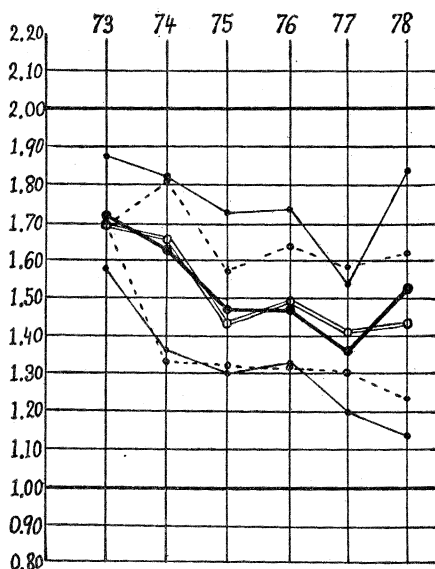


FIG. 11. Plot showing results obtained by running the Iowa strain of *Aphis. avenae* Fab. as a check on the Oregon strain to show the effects of long-continued parthenogenetic reproduction. The solid lines are for the fluctuations in the Oregon strain, the others for the Iowa strain. Plan of curves the same as in Figs 7, 8, and 9.

the continued parthenogenetic reproduction had reduced the virility of the experimental line obtained from a wild agamic female in Oregon.

A careful comparison of the Iowa forms with those of the seventy-third generation in my pure line showed no structural differences. They were somewhat different in coloration, being a deep, dark green, while those being used in the experiment were a light yellowish green. The cinnamon areas about the bases of the cornicles were well marked, but apparently were not so

extensive as those in the seventy-third generation of the experimental pure line.

One individual was isolated from those obtained in Iowa, and was started in the production of a check strain when the individual of the 1173 generation was selected for carrying on the experimental strain obtained from Oregon. The means obtained, and the lengths of the extreme variants of each fraternity are plotted in Fig. 11. The data for the Iowa check strain are given in tabular form in Table X. What results do we find when comparison is made between these two strains?

1. *In Regard to Size.*—By observing the plot showing the extremes and the mean of each of the fraternities we see that they very nearly coincide. The parent individual of the Iowa strain had a length very near that of the mean of the 1173 fraternity, which was the fraternity I was rearing at the time I obtained this stem parent. Of the five means obtained for the five fraternities of the Iowa strain, three were slightly above and two slightly below the means of the corresponding fraternities of the Oregon strain.

If we compare the average mean obtained from the fraternal means of the 5 check generations of the two strains, we have:

Average for the fraternal means: Oregon strain = 1.489 mm.

Average for the fraternal means: Iowa strain = 1.479 mm.

The difference between these two averages (one hundredth of a millimeter) is an insignificant difference when we consider the great range in variation found among individuals born of the same parent. We find, therefore, that as far as size is concerned there has been no dwarfing or indication of lack of vigor in growth due to the long continued parthenogenetic reproduction in the Oregon strain (the main pure line of *Aphis avenæ* Fab.).

2. *In Regard to Color.*—When first found the Iowa strain of *Aphis avenæ* showed a much deeper coloration than those individuals of the Oregon strain that had been bred for 73 generations in confinement. The individuals of the Iowa strain, however, lost these deeper colors immediately after being reared under the same conditions as those of the Oregon strain, and were undistinguishable from individuals of the latter strain. The fact that the individuals of the Iowa strain were more deeply

TABLE X.

## DATA FOR IOWA CHECK STRAIN.

Individual	Length in Millimeters	Fraternal Mean.
I <sub>21</sub>	1.57	
I <sub>22</sub>	1.81	
I <sub>23</sub>	1.73	
I <sub>24</sub>	1.34	
I <sub>25</sub>	1.77	
I <sub>26</sub>	1.66	
I <sub>27</sub>	1.59	
I <sub>29</sub>	1.59	
I <sub>210</sub>	1.57	
I <sub>31</sub>	1.41	1.625
I <sub>32</sub>	1.40	
I <sub>33</sub>	1.41	
I <sub>34</sub>	1.57	
I <sub>35</sub>	1.49	
I <sub>36</sub>	1.31	
I <sub>41</sub>	1.50	1.432
I <sub>42</sub>	1.49	
I <sub>43</sub>	1.44	
I <sub>47</sub>	1.31	
I <sub>48</sub>	1.64	
I <sub>51</sub>	1.59	1.476
I <sub>52</sub>	1.36	
I <sub>53</sub>	1.59	
I <sub>54</sub>	1.33	
I <sub>55</sub>	1.33	
I <sub>56</sub>	1.40	
I <sub>57</sub>	1.41	
I <sub>59</sub>	1.34	
I <sub>510</sub>	1.44	
I <sub>511</sub>	1.57	
I <sub>512</sub>	1.30	
I <sub>61</sub>	1.46	1.424
I <sub>62</sub>	1.24	
I <sub>63</sub>	1.53	
I <sub>64</sub>	1.61	
I <sub>65</sub>	1.34	
I <sub>66</sub>	1.60	
I <sub>67</sub>	1.33	
I <sub>68</sub>	1.40	
I <sub>69</sub>	1.41	
I <sub>610</sub>	1.49	
		1.441

colored when first found was probably due to the fact that they had been feeding on the leaves of the oat plants which contained much more chlorophyll than the tender shoots of wheat, upon which the individuals of the main pure line were being fed. At any rate the check experiment showed that they were not dependent upon a greater vigor or virility.

3. *Fecundity*.—From the data here obtained it is not easy to compare satisfactorily the fecundity of the individuals of the two strains. Six days was always the minimum time allowed for the development and production of young of each individual. Using this six-day life cycle schedule, however, we find considerable difference between the total number of individuals obtained from the five parents concerned. In the case of the Oregon strain 55 young were produced. In the case of the Iowa strain kept under identical conditions as a check, only 46 individuals were obtained. This gives for the average size of the fraternities of the Oregon strain 9.93 individuals, and for the fraternities of the Iowa strain an average of 7.44 individuals. We find, however, that one other factor enters into the results to such an extent as to make these findings of little value for comparing the relative fecundity of the two strains. This factor is the length of the period of development.

4. *Length of Period of Development*.—Of the 55 individuals obtained in the Oregon strain during the 5 test generations, only 2 failed to reach the paternity age in the 6 day period allowed. In the 46 individuals obtained at the same time in the 5 generations of the Iowa strain 8 individuals failed to reach the age of paternity in the 6 days allowed.

We find, then, that the Iowa strain developed much more slowly under the same conditions than the Oregon strain. I believe that the Oregon strain had changed its developmental period, since it was started about 2 years previously

What then was the effect of continued parthenogenetic reproduction for 73 generations in *Aphis avenæ* upon the virility of the strain? We find that by the means of comparison just reported no evidence of racial deterioration or loss of virility in any respect. We do find, however, strong evidences of adaptation in regard to the shortening of the growth period. Yet in

this regard we must remember that the Iowa strain with which this long-pedigreed Oregon strain was compared may have differed from the latter genetically. Our conclusions can not be final in regard to this point.

THE OPTIMUM TEMPERATURE FOR THE PRODUCTION OF WINGLESS  
AGAMIC FORMS, AND THE RELATION OF TEMPERATURE  
TO DIMORPHISM.

During the early stages of the propagation of isolation 11 it appeared best to determine with stock obtained from discards of this subline the optimum temperature for the production of wingless agamic forms, and to see if it was possible so to regulate the temperature that only wingless forms would appear. Experience had shown that the growth of certain generations had evidently been retarded by unusual temperatures, and to obtain an optimum for growth would hasten the breeding very materially, and at the same time furnish more stable conditions for the experiment. The appearance of occasional winged forms during the first score of generations caused a complete loss, as far as number of individuals used in the experiment was concerned, as none of these was measured. If these winged individuals could be prevented from appearing, and the line made completely monomorphic, a great gain would be accomplished.

Accordingly mothers were placed in a constant temperature cell, and the young were allowed to be born and reared at various constant temperatures. The cell, which admitted light, was so regulated by an electric thermo-regulator that it seldom varied either way more than  $0.2^{\circ}$  F. The temperatures at which these various individuals were born and reared were as follows:  $60^{\circ}$  F.,  $70^{\circ}$  F.,  $80^{\circ}$  F., and  $90^{\circ}$  F. At  $60^{\circ}$  F. all the individuals reared produced winged forms. At  $70^{\circ}$  F. only 15.1 per cent. were winged; at  $80^{\circ}$  F., 69.6 per cent. were winged, and at  $90^{\circ}$  F. no individual lived to reach the last nymphal stage.

From these results I judged that at  $65^{\circ}$  F., or slightly above that, probably only wingless forms would be produced; certainly only very few winged forms should appear. These predictions were correct, for in the next 20 generations I so regulated the temperature for isolation 11 that not a single winged individual

appeared. Temperature changes alone, therefore, are capable of affecting dimorphism. Upon the tender shoots of wheat I produced either winged or wingless forms at will. It was a surprise to me to find that both extremes of temperature caused the appearance of the winged forms, and suppressed apparently the appearance of wingless forms.

How did these different temperatures affect the growth period of the wingless individuals? At 60° F., no wingless forms were produced; at 70° F. the average period of growth was 6 days;

TABLE XI.

DATA SHOWING EFFECTS OF VARIOUS CONSTANT TEMPERATURES ON APHIS AVENÆ FAB.

	At 60° F.	At 70° F.	At 80° F.	At 90° F.
Average daily birth rate per individual.	2.2	3.7	6.1	0.25
Length of developmental period for wingless form.....	—	6 days	7 days	12+days
Length of developmental period for winged form.....	14½ days	9½ days	7½ days	—
Mean length of adult wingless forms...	—	1.155 mm.	1.246 mm.	—
No. of individuals used.....	44	37	61	5
Percentage of individuals winged.....	100.	15.1	69.6	—
No. of individuals reaching maturity...	12	11	46	0
Percentage of mortality.....	72.7	70.3	24.6	100.

at 80° F., 7 days; at 90° F., 12+ days. It appears from this that the optimum temperature for the growth of wingless individuals is very nearly the same as the optimum temperature for the production of the same kind of individuals. It may be these two optima are the same.

The results of these experiments with constant temperatures, which gave additional data soon to be considered, are given in tabular form in Table XI.

#### THE EFFECT OF TEMPERATURE ON GROWTH, SIZE, REPRODUCTION, AND MORTALITY.

While starting the constant temperature experiment primarily to determine the optimum for the production of wingless agamic forms, it appeared profitable to observe also the effects of different constant temperatures on growth, size, reproduction and mortality.

*Sources of Error.*—Although there were important changes in humidity during these constant temperature experiments, yet, as has already been stated, Headlee has shown that changes of humidity from 37 per cent. to saturation are without effect upon the metabolism of plant lice. As for light changes, it is probable that metabolism was to some extent affected by these, but experience with other insects has shown that unless these are quite marked (*e. g.*, bright sunlight or total darkness) the effects are not great. There was no change in the food, unless perhaps the changes in temperature themselves changed somewhat the nature of the food derived from the wheat shoots.

The results obtained showing the effects of the four constant temperatures employed; 60° F., 70° F., 80° F., and 90° F., are given in tabular form in Table XI.

1. *As to Growth.*—At 60° F. it took the winged forms 14½ days to reach maturity (this being the average for all individuals reared). No wingless forms were produced at this temperature, so that we have no data upon the growth period for this form at this period. At 70° F., the wingless forms reached maturity in 6 days, the winged in 9½ days. At 80° F., the wingless forms reached maturity in 7 days, the winged in 7½ days. At 90° F., no nymphs of the winged forms had reached maturity in 12 days. No nymphs of wingless forms were observed at this temperature, and all the individuals used died before reaching maturity. The optimum temperature for growth, therefore, must be different for the two forms. For the wingless forms it probably is a little above 65° F. as before stated, but in the case of the winged forms is somewhere near 80° F.

2. *As to Size.*—Only two records for the size of adult wingless forms were obtained. The mean for those reared at 70° F. was 1.155 mm., and for those at 80° F., 1.246 mm. Both these means are below the mean of the pure line stock from which the mothers were taken, and far below the mean! Can it be that constant temperatures, no matter at what degree, have a dwarfing effect on plant lice? Does the changing of temperature stimulate growth and metabolism in general? These are interesting problems for further investigation. The results obtained in this experiment appear to show that such dwarfing actually does take

place at ordinary temperatures if the temperature is kept constant.

3. *As to Rate of Reproduction*—At 60° F. the average rate of reproduction was 2.2 births per day per individual. At 70° F. the rate was 3.7 per day per individual. At 80° F. the rate was 6.1 and at 90° F., 0.25. Therefore, we conclude that temperature affects the rate of reproduction in a most fundamental way; that about 80° F. is the optimum temperature for reproduction; and, that the optimum for reproduction is quite different from the optimum for growth, at least as far as the wingless forms are concerned.

4. *Effect on Mortality*.—The mortality percentages for the different constant temperatures were: 60° F., 72.7; 70° F., 70.3; 80° F., 24.6; 90° F., 100. Obviously, the extremes of temperature are quite disastrous to *Aphis avenæ*. At 60° F. we find that almost 3 out of 4 die before reaching maturity. At a constant temperature of 90° F. not a single individual reached maturity. This observation coincides well with observations in general of specialists in the Aphididæ, who report the disastrous effects of hot summer weather on our injurious species. The optimum for the least mortality appears to near 80° F., but probably it is slightly below this point.

#### THE EFFECT OF FASTING, DURING THE GROWTH PERIOD, ON THE SIZE OF ADULTS.

The abundance of food during the growth period of an insect is known frequently to affect the size of the adults produced. It occurred to me that probably fasting periods of different lengths during the growth of individuals of *Aphis avenæ* Fab. might affect the size of the adults. In order to test this point, 33 young nymphs, born between 6:00 and 12:00 A.M. (average time of birth 9:00 A.M.), were placed in different lots in four different breeding cages, but under similar conditions, and were deprived of food for different periods. The individuals of all lots were allowed to feed for 24 hrs., then they were deprived of food for the following periods: Lot 1, 4 hrs.; lot 2, 8 hrs.; lots 3 and 4, 24 hrs. At the end of these fasting periods it was found that the individuals of lots 3 and 4 were dead. The others endured their



shorter fast and were placed back on their succulent wheat shoots in order that they might complete their development. Of those in lot 1, 2 individuals reached maturity, and of those in lot 2, 4 individuals reached maturity. The average time required for the individuals of these two lots to reach maturity was 5 days in both cases. Quite normal. They were all wingless forms, and gave the following measurements for length: Lot 1, 1.00 mm. and 0.89 mm.; lot 2, 0.96 mm., 0.99 mm., 0.97 mm., and 1.00 mm. The mean lengths for the two lots were: Lot 1, 0.945 mm.; lot 2, 0.980 mm. Both are much below the mean for the line.

TABLE XII.

DATA FOR EXPERIMENT ON EFFECT OF SINGLE FASTING PERIODS ON SIZE OF ADULTS.

Lot No.	No. Individuals in Lot.	Period in Which Birth Took Place.	Average for Date of Birth.	First Feeding Period.	Length of Fast.
1	4	6.00 to 12.00 A.M.	9.00 A.M.	24 hrs.	4 hrs.
2	7	6.00 to 12.00 A.M.	" "	" "	8 hrs.
3	6	6.00 to 12.00 A.M.	" "	" "	24 hrs.
4	10	6.00 to 12.00 A.M.	" "	" "	24 hrs.

TABLE XII.—*Continued.*

Lot No.	First Individual Adult.	Last Individual Adult.	Length of Life Period, Average.	Winged or Wingless.	Mean Length for Lot, in Mm.
1	Jan. 8, 9 A.M.	Ja. 8, 9 A.M.	5 days	All wingless	0.945
2	" "	" "	"	" "	0.980
3	All dead				
4	All dead				

From this we conclude that single fasts during the development of *Aphis avenæ* Fab. do not necessarily change the length of the period of development, but greatly reduce the size of the adult individuals produced. Data for this fasting experiment are given in tabular form in Table XII. It will be noticed that all the individuals produced in this experiment were wingless forms.

#### THE RANGE AND NATURE OF VARIATION IN A PARTHENOGENETIC PURE LINE.

Variation in a parthenogenetic pure line presents all the essential features that it does in nature in general. Probably the one thing that impresses one more than anything else in

regard to variations in a parthenogenetic pure line is the great predominance and great range of fluctuating, or individual, variations; including under this head the variations in parts of the body as well as variations affecting the whole of it. These are the omnipresent, the conspicuous, and, I am tempted to state, the characteristic variations in a parthenogenetic pure line. It is true that we occasionally find an abrupt, or spontaneous variation, but such variations are rare, and as a rule are in the nature of omissions of parts or the arrest of the development of the whole or a part of the individual. Fluctuating variability has been shown by several workers to be greater where amphimixis does not take place. Walton<sup>1</sup> has shown this conclusively for *Spirogyra*. Hence, we may assume in the pure line of *Aphis avenæ* here considered that the absence of amphimixis is a fundamental reason for the great range in fluctuating variability.

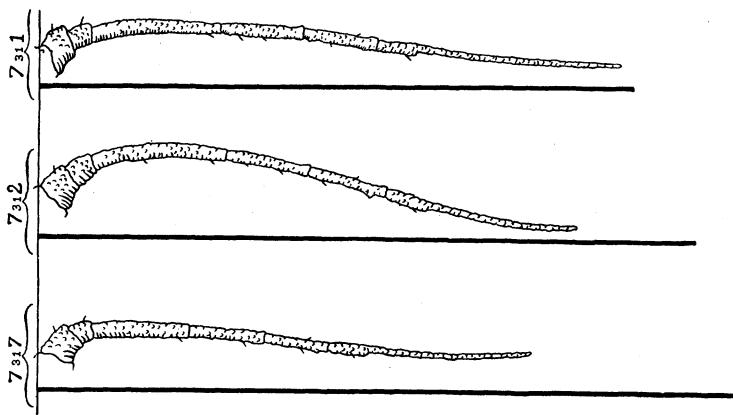


FIG. 12. Camera lucida drawings, all of the same magnification, showing extremes of fluctuating variation in the lengths of the right antennæ of three individuals (7311, 7312, and 7317) of the 731 fraternity. The heavy black line in each case represents the body length, same magnification, of the individual whose antenna is drawn by the side of it.

The range of fluctuating variability is frequently so great among the individuals of a single fraternity as to be quite noticeable to the eye without measurements being made. In Fig. 12 we have camera lucida drawings, all of the same magnification of the right antennæ of three individuals of the 731 fraternity. Also

<sup>1</sup> Walton, L. B., 1915, "Variability and Amphimixis," *Amer. Nat.*, Vol. XLIX., pp. 649-687.

by the side of each antennal drawing is a heavy line representing the length of the individual possessing the antenna, also magnified to the same degree as the antenna itself. In the case of individual 7<sub>31</sub>1 the antenna is practically of the same length as the body. In the case of 7<sub>31</sub>7 the antenna is considerably less than two thirds as long as the body. All intergrades were found between these two extremes, showing that these variations are only fluctuations.

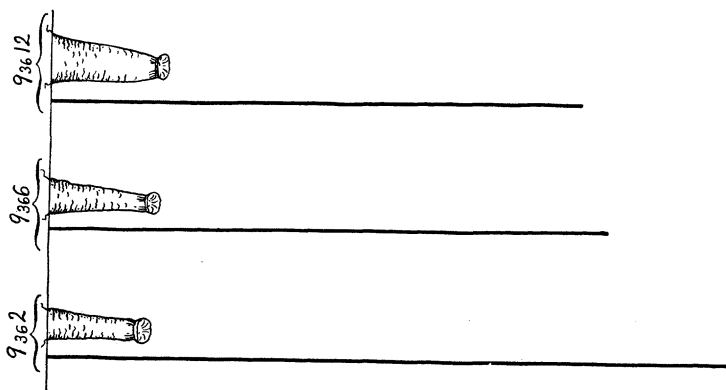


FIG. 13. Camera lucida drawings, all of the same magnification, showing extremes of fluctuating variation in the lengths of cornicles from three individuals (9<sub>36</sub>12, 9<sub>36</sub>6, 9<sub>36</sub>2) of the 9<sub>36</sub> fraternity. The heavy black line in each case represents the body length, same magnification, of the individual whose cornicle is drawn by the side of it.

Fig. 13 shows us a similar variation in the length of the cornicles in comparison with the length of the body in a single fraternity. The cornicles of individual 9<sub>36</sub>12 (the left of which is shown at top of Fig. 13) are 25.5 per cent. of the total body length of the same individual. The cornicles of individual 9<sub>36</sub>2 (one of which is represented at the bottom of Fig. 13) are only 17.3 per cent. of the body length of this individual.

The variation in the relative size of contiguous parts is shown in Fig. 14, where we have represented camera lucida drawings, all of the same magnification, of the third and fourth segments of the antennæ of three different individuals of the F<sub>9</sub> fraternity. Here the large segments are the third and the small ones the fourth. Observe that there is almost no variation in the length

<sup>1</sup> The letter *F* is here used to denote the subline or isolation, and refers to isolation No. 3 (only one isolation was running during the ninth generation).

of the fourth segment, but a great variation in the length of the third. In  $F_9I6$  the third segment is not more than a fourth longer than the fourth segment; in  $F_9I5$  the third segment is almost twice as long as the fourth one.

Variation in size is probably as noticeable as any other of the fluctuating variations. In Fig. 15 we have drawings of the same magnification of two individuals obtained in isolation II of

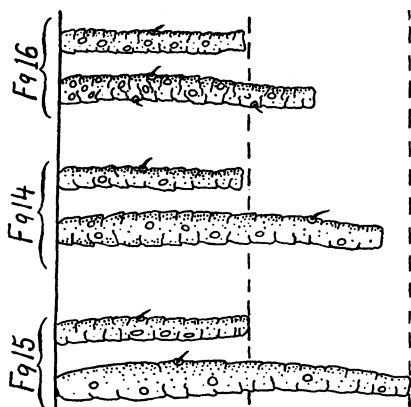


FIG. 14. Camera lucida drawings, all of the same magnification, showing the extremes of fluctuating variation in the length of the third as compared with the fourth segment of the antenna of three individuals of a single fraternity ( $F_9$ ). The third (long) and fourth (short) segments of an antenna of a single individual are drawn together to same scale.

the pure line of *Aphis avenæ*. The larger figure is of individual  $II_{501}$ , length 1.99 mm.; the smaller one of  $II_{588}$ , length 0.99 mm. In other words one individual is slightly more than twice as long as the other, and from this we should judge it to be about 8 times as heavy (the two not being weighed). These are the extremes obtained in 459 individuals, representing all those obtained during the first 40 generations of isolation II.

Not only do we find fluctuations in regard to size in the individual and its parts, but in shape also. In Fig. 16 we have drawings of the right cornicles of three individuals of the  $4_{27}$  fraternity. What a variation in shape! In the case of the right cornicle of  $4_{271}$  we find the base almost twice as broad as the distal end. In the right cornicle of  $4_{274}$  the base is no wider than the distal end. This latter cornicle is strongly incrassate at its tip,

while the former is not at all incrassate. Yet frequently the incrassate nature of the cornicles has been used as a generic character!

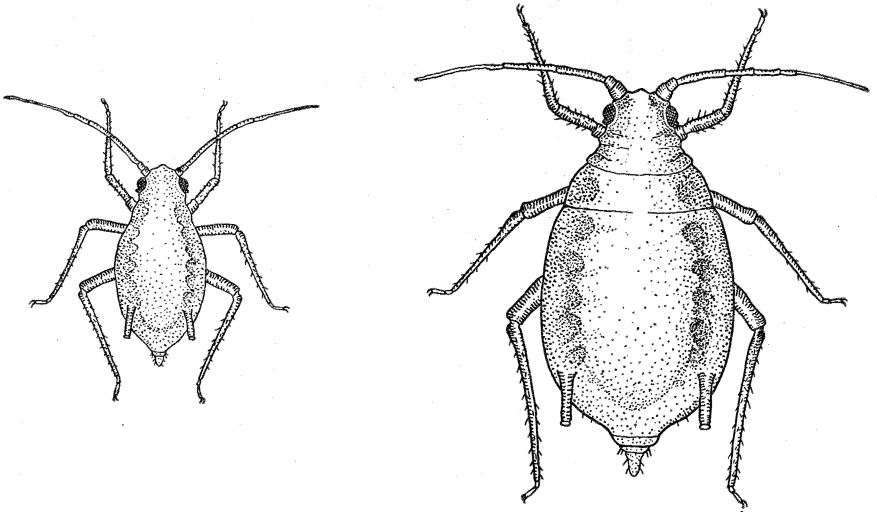


FIG. 15. Camera lucida drawings of same magnification showing extreme fluctuations in size of two individuals of isolation No. 11. The larger individual is 11501; the smaller 11588.

Do these fluctuating variations group themselves about a common mean as such variations normally do? Apparently

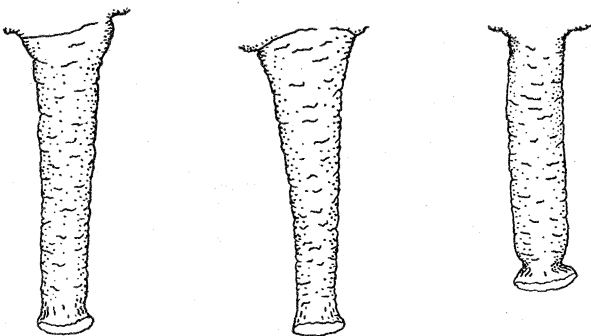


FIG. 16. Camera lucida drawings, all of the same magnification, showing the extremes of fluctuating variation in the shape of the cornicles of three individuals (4273, 4271, and 42711) of the same fraternity.

yes. In Fig. 17, I have plotted the frequency polygon for the character of body length for the 477 individuals obtained in

isolation II. Notwithstanding the selection made in this subline we find the typical unimodal frequency polygon (shown by the heavy unbroken line) representing the normal variations of a fluctuating character.

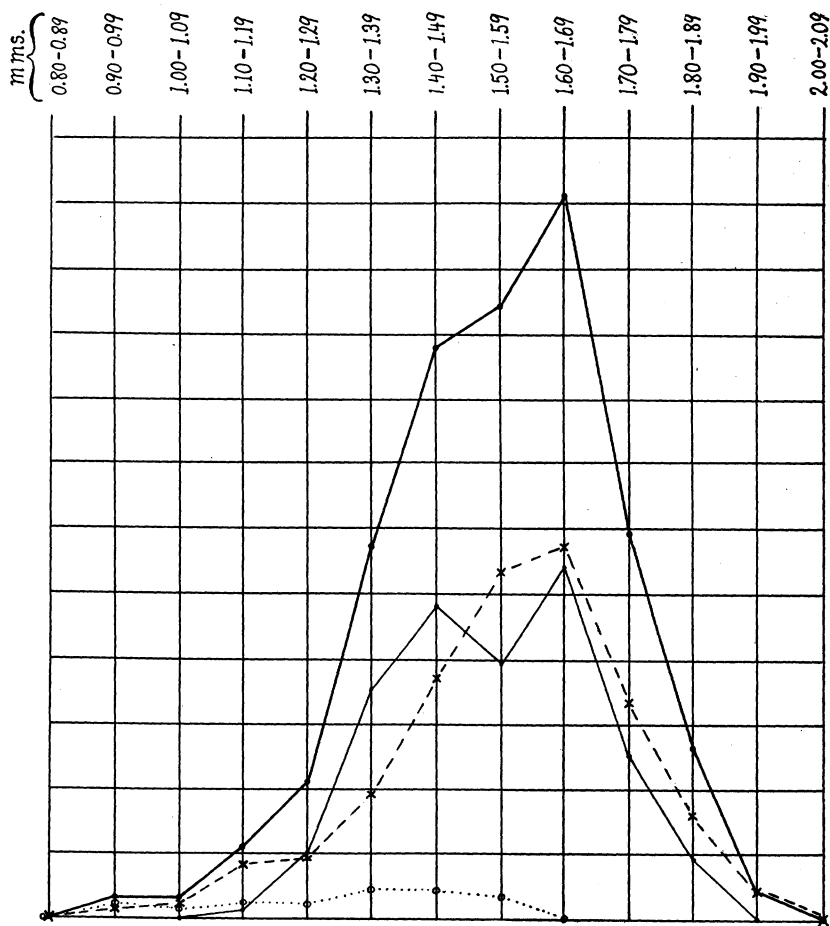


FIG. 17. Frequency polygon to show variations in body length for the 477 individuals obtained in isolation No. II. The polygon is broken up into three components representing the frequency polygons for the first score, second score, and last four generations of this isolation. For further explanation see text.

The causes for the variation in fluctuations have not been well understood in most instances. De Vries maintains that in plants they depend probably exclusively upon nutrition. I find that

in plant lice temperature as well as nutrition is the cause of fluctuations in body length. The effect of temperature on the variations in body length is well shown in Fig. 17. The large frequency polygon represented by the heavy broken line at the top can be analyzed into three components representing respectively the frequency polygons for the first score, second score, and last four generations of isolation 11. The broken line describes the frequency polygon for the first score of generations where no control was made over temperature conditions. The light unbroken line describes the frequency polygon for the second score of generations where the temperature was so regulated about the optimum for the development of wingless forms that only wingless forms appeared. The dotted line toward the bottom represents the frequency polygon for the last four generations where the individuals were reared on much older wheat plants.

In studying the curves for the first and second scores of generations we note no change of the mean for body length which in both cases is a little less than 1.65 mm., but by observing the bases of these two polygons we find the extremes of variation in body length to be much greater in the case of the one for the first score of generations when the extremes of temperature were also much greater.

When a change was made in the nature of the food (temperature being left the same) we find a shifting of the mean (see lower polygon in Fig. 17) for body length. It no longer is near 1.65 mm., but is between 1.35 and 1.45 mm.

But fluctuating variations were not the only kinds observed in the pure line of *Aphis avenæ*. Some abrupt variations were also observed. These abrupt, or discontinuous, variations were, however, very rare in the pure line of the grain aphid. I found only four that were quite noticeable. One of these was a dropping out of the branch of the sector of the third discoidal vein in the anterior wings of the winged form, another the dropping out of the sector itself; the third, an addition of one or more cross veins to the bifurcating branches of the sector of the third discoidal vein; the fourth, the complete arrestment of development of the individual during the third or fourth nymphal stages.

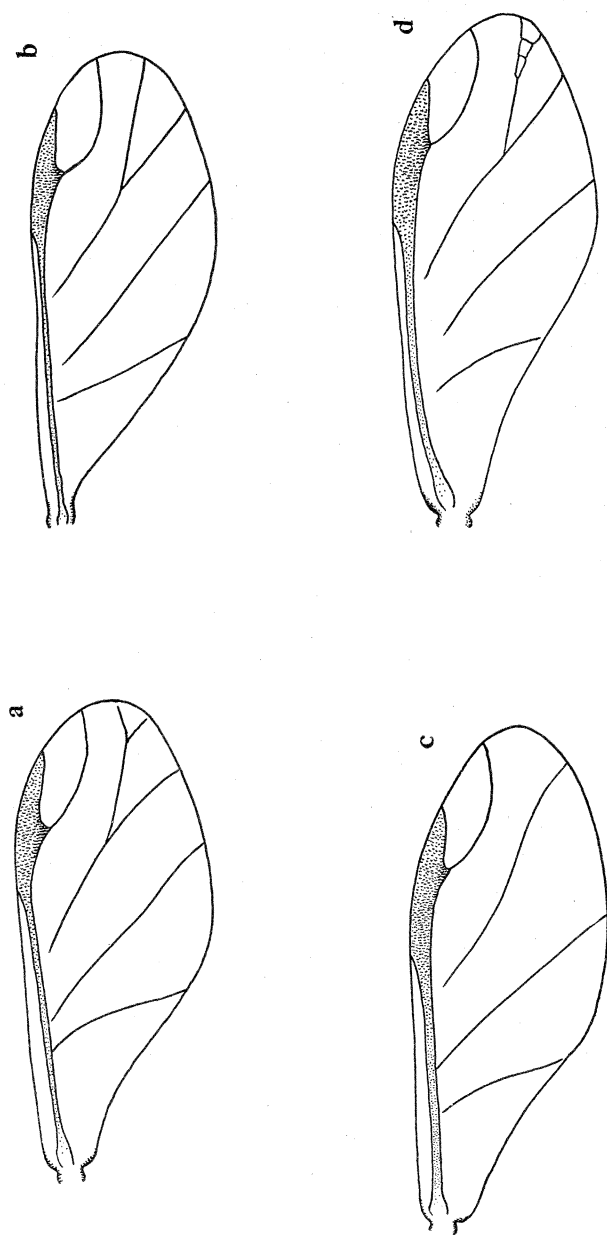


FIG. 18. Abrupt, or discontinuous variations in the pure line of *Aphis avenae* Fab. A. Wing of winged form showing the normal branching of the third discoidal vein. B. Branch to sector of third discoidal vein missing. C. Sector itself wanting. D. Two cross veins between branches of sector of third discoidal vein.



I only studied the transmissibility of the latter abnormality. Where individuals stopped completely their development in any nymphal stage, they always produced normal young, and in every case these young grew to normal adults. The arresting of the development of these nymphs caused them to become pædogenic. The pædogensis, however, was never fixed. Several of these pædogenic nymphs appeared. Some of them were nymphs of wingless form, and some of the winged form. The cause of the arrested development I did not learn, but it may have been due to low temperatures.

The variations mentioned in the third discoidal vein are shown in Fig. 18. I hope some time to test the transmissibility of these abnormal wing characters. The variation shown in *B* is quite common. The variations shown in *C* and *D*, on the other hand, are rare. In regard to the variations of this third discoidal vein, it should be mentioned that frequently the venation of the wing on one side of an individual will be different from the venation of the wing on the other side of the same individual. Yet there is a tendency for the anomaly to appear simultaneously on both wings of the same individual.

### THE OCCURRENCE OF PÆDOGENESIS.<sup>1</sup>

The occurrence of pædogensis (the reproduction parthenogenetically by immature instars) is a phenomenon known to be well established in the genus *Miastor* (Fam. Cecidomyiidae), and occurs also in a few of the species of *Chironomus*. But pædogensis is extremely rare in the animal kingdom, and as far as the writer can learn has not been recorded as occurring erratically in plant lice.

In the course of my experiments with *Aphis avenæ*, which covered about two and a half years, I observed on several occasions individuals that never passed beyond their third or possibly fourth nymphal instar, but nevertheless began and continued to reproduce in a normal manner. These pædogenic

<sup>1</sup> The word pædogensis is here used in a broad sense denoting parthenogenetic reproduction by any immature stage of an animal that passes through a metamorphosis. Nymphal pædogensis does not have nearly as deep a significance as larval pædogensis that is found in some insects which pass through a complete metamorphosis.

nymphs were of both forms (the wingless and winged), and in every instance their young gave only normal adults, and had so far as could be ascertained had normal reproductive powers. I shall here record some data obtained in regard to these pædogenetic nymphs.

One of the first pædogenetic individuals observed was 3195. This nymph was of the winged form and never passed beyond the last nymphal stage. It was born from 3185 along with 13 other young. It reached its final nymphal form at the time that two of its sisters reached their normal maturity. This pædogenetic nymph gave birth to 8 young the first day of reproduction, 4 the second, none on the third and fourth days, and was killed on

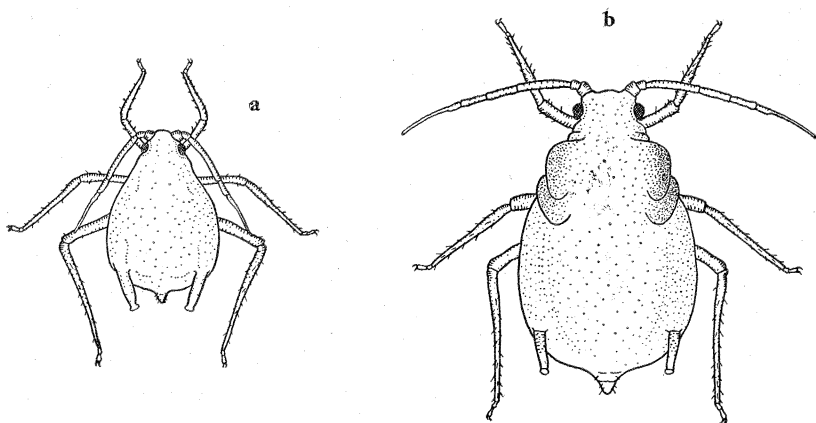


FIG. 19. Pædogenetic nymph of *Aphis avenæ* Fab. A. 32410, a pædogenetic nymph of the wingless form. B. 11410, a pædogenetic nymph of winged form.

the fifth day. Of the 12 offspring left, 3 reached maturity. They were normal wingless forms, and differed in no perceptible way from the many other wingless forms at hand. These three normal adults each gave many young, which, however, were not reared to maturity.

Another pædogenetic nymph to appear was 32410 (see Fig. 19, a), which was a pædogenetic third nymph of the wingless form. It was one of the 12 offspring of 3231, a normally winged adult. Of the 11 sisters of this pædogenetic form, 10 reached maturity, and all proved to be normal wingless forms. This pædogenetic nymph gave birth to 3 young before it was killed. These young, however, were discarded because of lack of time to care for them.

But the most noteworthy case of erratic pædogenesis was found, however, in the offspring of 11<sub>48</sub>5, a normal wingless adult, that left 13 young. Of these 13 young, 9 reached the stage of maternity. Of these 9, 3 were pædogenetic, 11<sub>49</sub>1, 11<sub>49</sub>2, and 11<sub>49</sub>5. These pædogenetic nymphs were all of the winged form, and reached their stage of reproduction along with the adults of the wingless form, which is much sooner than the time allowed for the development of the normal winged adult forms. The pædogenetic nymphs were all large, vigorous individuals, and reproduced normally. The individual 11<sub>49</sub>1 gave 11 young before she was killed. Of these young, 1 was reared to maturity, producing a normal wingless adult. Another, 11<sub>49</sub>2, gave 14 young before being killed, and of these, 13 were reared to maturity, producing in every case normal wingless adults. The third individual, 11<sub>49</sub>5, gave birth to 16 young before being killed, of which 4 were reared to maturity, all being normal wingless forms.

Other instances of erratic pædogenesis were met with, but these suffice to show the nature of their appearance, and the fact that this tendency toward pædogenesis is not inherited. Pædogenesis in this pure line appeared to be due to the arrestment of the growth of the immature individual, the development and functioning of the reproductive system being unhindered. It was probably induced by low temperature changes during a critical period in the development of the individual. At any rate adverse conditions must have been responsible for this arrested development.

## SUMMARY OF RESULTS.

### *In Regard to Heredity.*

1. Six different fluctuating variations in a parthenogenetic pure line of *Aphis avenæ* Fab. were tested to see if there was any summation effect of selection on these variations. Selections were made for ten or more successive generations in the case of three of these characters for forty-four successive generations in the case of one character; and were carried out in both plus and minus directions in the case of two characters. In all of these cases no summation effect was produced by selection.

2. The results of this work with *Aphis avenæ* Fab. are, we believe, sufficient to warrant the following generalization: Fluctuating variations in a parthenogenetic pure line of *Aphis avenæ* Fab., and presumably in all parthenogenetic pure lines, are in general not dependent upon germinal variations, and for this reason are not capable of increase or summation through the action of continued selection. Or to put it in another way: Fluctuating variability in a parthenogenetic pure line is devoid of one of its most important causes when exhibited in higher animals that reproduce sexually—that is, germinal variability.

3. *Corollary*.—Some investigators, not considering the original limitations that were placed on the pure line theory, *i. e.*, that it applies only to forms that reproduce asexually or by self-fertilization, have attempted, and disastrously, to apply its principles to sexually reproducing animals. This has been unfortunate, and has added confusion to controversy, and has been wholly unnecessary. Castle's work with hooded rats<sup>1</sup> has shown conclusively that germinal variability is to be assigned as the cause, of a part at least, of phenotypical variability in these higher forms, thus exempting them from the scope of the pure line theory.

4. Selection from extreme variants within a pure line of *Aphis avenæ* Fab. is without effect upon the somatic characters of succeeding generations.

5. Long-continued selection from the extreme variant in each succeeding fraternity produces no more of a change in the mode of the variable than selection from individuals but slightly different from the mean of the line and for only a few generations. Neither produces any perceptible change.

6. The pure line theory applies to parthenogenetic arthropods as well as to forms that reproduce by budding, fission, or self-fertilization.

7. Selections from extreme variants for 44 consecutive generations, using a character that is well known to be inherited in higher animals that reproduce sexually, failed to shift in the least the mean for the line.

<sup>1</sup> See Castle, W. E., 1915, "Some Experiments in Mass Selection," *Amer. Nat.*, Vol. XLIX., pp. 713-726.

8. Where selections were made in opposite directions (plus and minus) in two isolations, each being used as a check against the other, it was found that the fluctuations were simultaneous in both isolations, and in the same directions, being thus independent of the effects of selection.

*In Regard to General Biology.*

9. Fluctuating, or individual variations, are of great magnitude, even in a single fraternity of a pure line of *Aphis avenæ* Fab., and are frequently different on the two sides of the same individual.

10. Abrupt, or discontinuous variations are very rare in a pure line of *Aphis avenæ* Fab., and the few that were observed were not proved to be inherited.

11. The variations in stature, or body length in *Aphis avenæ* Fab. are due largely to variations in temperature and food.

12. The optimum temperature for the production of wingless agamic forms in *Aphis avenæ* Fab. is about 65° F., and the percentage of winged forms produced increases in accord with the degree of divergence both above and below this optimum.

13. Only wingless agamic forms are produced at a mean average daily temperature of about 65° F.

14. A constant temperature of 90° F. is sufficient to prevent completely the development of *Aphis avenæ* Fab.

15. Long-continued parthenogenetic reproduction did not affect the size, color, or fecundity of the strain of *Aphis avenæ* Fab. used. The period of growth was somewhat shortened. This may have been an adaptation, or response of the strain to the artificial, suboptimum and almost constant conditions under which they were kept.

16. Pædogenesis occasionally occurs in *Aphis avenæ* Fab., both among the nymphs of the winged form and nymphs of the wingless form. It is due to the arrested development of the body in general, while the reproductive organs become completely functional. All offspring of these pædogenetic nymphs that grew to become adults were normal.

17. Fluctuating variations are the omnipresent, the conspicuous, and in fact the characteristic variations in a pure line of plant lice, and, as have before stated, they were not shown to be inherited.